PLANT ECOLOGY

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PREFACE

This volume is designed to meet the need for a comprehensive textbook of plant ecology and to furnish a guide to workers in related fields. It is written from the standpoint of development, instrumentation, and experiment. The student of plant production, whether in botany, agriculture, grazing, forestry, plant pathology, or other fields, is beginning to study more thoroughly the intimate relations between plants or groups of plants and their environment. In fact, many of his most important problems deal with the relations of plant to habitat, whether the latter be natural or modified by cultivation, and these can not be satisfactorily solved until these relationships are well understood. In addition, the field of ecology is unique in its fundamental contributions to a general understanding of the plant world upon which man and animals are dependent. This book has been planned to meet these several needs. It is the outgrowth of many years of research and teaching by both authors, and comprehends the general course in ecology given by the first-named author in the University of Nebraska. The subject matter has been repeatedly used by classes and found readily comprehensible; the experiments and exercises have proved workable, and the field work illuminating.

The experiments and exercises for greenhouse and laboratory have been outlined in detail as an outcome of repeated use by classes. More experimental work has been included than the average class will find time to do and, thus, a choice of materials may be had to fit the time and conditions under which the course is given. Field studies have been suggested only in broader outlines. While all of this work is usually done, the details are left to be elaborated for the particular communities available to the student.

The writers are under great obligations to the Carnegie Institution of Washington for the liberal use of text and illustrations from several publications and to Henry Holt and Company for similar permission in connection with "Plant Physiology and Ecology." To a number of students of the first-named author, especially Mr. T. L. Steiger and Miss Theodora Klose, the writers are indebted for certain drawings. The

chapter on Soils has been carefully read by Prof. J. C. Russel, and the entire manuscript by Dr. Herbert C. Hanson. The writers are further indebted to Prof. T. J. Fitzpatrick and Dr. Walter J. Himmel for the reading of both manuscript and proof.

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TO THE TEACHER

(CONCERNING WORK IN THE FIELD)

Plant ecology is preeminently a field subject. No type of class work needs more careful planning than does that given in the field. Although the first-named author has taught ecology for many years, he seldom takes a class into the field without making a preliminary visit for the purpose of formulating a detailed plan. When carefully outlined, enough field experience may be gained during 8 to 10 half-day trips to afford a fairly adequate background for study during the winter. To illustrate, at Nebraska the first field trip usually has for its purpose the study of about 10 dominants and subdominants of low and high prairie, respectively, including something of the autecology of each. It is concluded by securing soil samples from the two habitats for water-content determinations.

A second half-day is spent in a brief survey of the important species of areas of upland prairie, tall marsh-grass swamp, and sumac thicket. Measurements of evaporation, humidity, and wind velocity in each community are supplemented by readings from cut-shoot potometers for a part of the period.

A study of salt-marsh dominants, their autecology, distribution in zones due to varying alkalinity, and successional relations from bare area to stabilized prairie, together with the securing of soil samples for later salt-content analysis, occupies another half-day.

Usually an entire day is spent in the forest, where especial emphasis is placed upon the recognition of various kinds of communities, *e.g.* hazelnut-coralberry chaparral, bur oak-bitternut hickory, shellbark hickory, and red oak-linden upland communities, and elm-ash flood-plain forest. Attention is directed toward a study of the conditions of soil, water content, etc. under which each develops; the structure of each community as regards important species, layering, and rate of growth of dominants as determined by an increment borer; the reactions of the community upon light, humus accumulation, and soil structure; and the relations of one community to another in their successional sequence.

The story of a hydrosere, beginning with an examination of submerged and floating plants, including bulrush, cattail, and reed swamp, and ending with the development of sedge meadow into climax prairie, occupies another half-day. Even in so brief a time much may be learned concerning the autecology of the dominants, their adaptations to the

habitat, the community reactions, and the resulting shifting of populations in the processes of development.

A visit to carefully selected rock outcrops affords opportunity for tracing the several stages of a xerosere. The ecesis and competition of crustose and foliose lichens are observed; the invasion of xeric mosses and the disappearance of the lichens; the establishment of pioneer herbaceous species where a thin soil has been formed; the development of the xeric herbaceous stage with the deepening of the substratum and humus accumulation; invasion of shrubs and their profound reactions resulting in the disappearance of the herbs and later in the invasion of drought-resistant trees. This includes a study of water- and humus-content of soil.

At least one-half day is given to learning the method of making list and chart quadrats and belt transects, usually in open areas. This includes examination of bisects found along steep roadside cuts or elsewhere.

One trip is concerned with the problems of grazing; indicators of various degrees of overgrazing are studied; the vegetation in exclosures, one to several years old, is compared and succession traced from greatly overgrazed, weedy, eroded areas to the climax vegetation. Later the changes as recorded by permanent quadrats, community maps, and photographs are examined and discussed.

Two stations are established near or on the campus where students operate hygrothermographs, soil thermographs, atmometers, and anemometers. The instruments are frequently checked and their operation continued until each student is familiar with all. This also includes the measurement of light intensities in several habitats. Little time is given to comparing and interpreting the records until the several factors measured are studied in detail.

During the field work, soil samples are secured for pH determinations, various living plants are transferred from field to greenhouse where they furnish material for the work on ecological anatomy, experiments on aeration, relative transpiration, length of day, etc. The field work of spring and summer need not be outlined here. A discussion of the text should present so many problems concerning instruments, phytometers, methods of studying vegetation, pollination, life histories, coactions, indicators, etc., that the question is one of doing what seems most important and expedient in the time allotted for the work.

Meteorological instruments and apparatus may be obtained from Julien P. Friez and Sons, Belfort Meteorological Observatory, Baltimore, Maryland, and Henry J. Green, 1191 Bedford Avenue, Brooklyn, New York. The more strictly ecological instruments are supplied by Fred C. Henson, 3628 East Colorado Street, Pasadena, California.

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PLANT ECOLOGY

CHAPTER I

VEGETATION; ITS ORIGIN, DEVELOPMENT, AND STRUCTURE

Vegetation is the sum total of plants covering an area. It may be a forest with its trees, undershrubs, and herbs and the forest floor with mosses, fungi, and lichens. It may consist of bulrushes, cattails, and

FIG. 1.—A layer of herbs, touch-me-not (*Impatiens*), three-seeded mercury (*Acalypha*), etc., in a young oak-hickory forest.

similar groups of plants growing in marshes, or of algæ submerged in water, or of the sparsely spaced cacti, sagebrush, etc., of the desert, or of the crust-like growth of lichens on otherwise bare rocks.

Vegetation is more than the mere grouping of individual plants. It is the result of the interactions of numerous factors. The effects of the plants upon the place in which they live and their influence upon

each other are especially significant. When trees develop in an area, they greatly modify conditions for growth by decreasing light and lessening the force of the wind (Fig. 1). Water evaporates less readily from the soil when covered with a mulch of decaying leaves, and the air is more humid under a leafy forest canopy. Sun-loving shrubs and herbs disappear and are replaced by those which thrive in cool, moist, shady places. The trees not only largely determine the kind of plants which grow beneath them but also profoundly influence each other. If densely crowded, they grow tall and straight and usually lose their lower branches

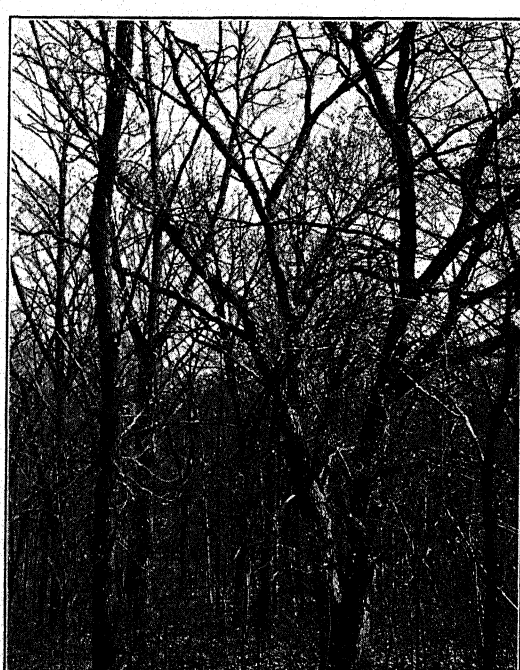

Fig. 2.—Much-branched bur oak about 140 years old which grew for nearly a century in an open area in eastern Nebraska. The tall, straight oaks growing around it are only about 50 years old. They have developed since the cessation of prairie fires.

as a result of insufficient light. Under such conditions, many species of trees can not thrive. Where the forest is open, the branches extend more widely and each individual makes a better development (Fig. 2). A study of vegetation reveals that it is an organic entity and that, like an organism, each part is interdependent upon every other part.

How Vegetation Originates.—Vegetation arises from the coming together of individual plants and their interactions upon each other. The latter are brought about by the plants modifying the habitat or place in which they live. They cause it to become wetter or drier; they

may increase the richness of the soil and decrease the light. In different ways, they make it a fit or an unfit place for various other kinds of plants to grow.

The origin of vegetation may be observed in a fallow field or garden. When all the former vegetation has been destroyed and seeds or other propagules buried too deeply to develop new plants, the area is usually populated very sparsely the first season, mostly with weedy annuals. By the second year, vegetation has greatly increased. In addition to a new crop of annuals, many biennials and even some perennials appear. These increase both by seed and vegetative propagation and with other plants that have migrated into the new area soon cover the ground and apparently appropriate all of the space. In the struggle for light, water, and nutrients that follows, the annuals, which must start anew each year, show their handicap by disappearing, while perennials, which constantly hold the ground and extend their territory, increase in importance. Some are more successful than others and in time occupy the area more or less exclusively.

An abandoned field or unused road in the Great Plains passes through these various stages and after many years is revegetated with buffalo grass and grama grass.[463] In New England or Kentucky the final vegetation is a forest. Sand dunes are vegetated in a similar way, by the coming together or aggregation of individual plants; so, also, are shallow ponds or dried lake bottoms, talus slopes, mud-covered flats, exposed rock ledges, and, indeed, all bare areas. Just as bare areas are being covered by plants today, so, too, they were vegetated in the past. Plants became grouped in the areas left bare by retreating glaciers, on the wind-blown hills of loess, on the uplifted margins of the ocean, and on the mountain ranges of naked rock. In short, vegetation originated with the appearance of the land mass that it covers.

How Vegetation Develops.—The development of vegetation consists of a number of closely related processes so important that each forms a special field for study. After the establishment of the first scattered invaders, the individuals come to be grouped, as a result of propagation, a process termed *aggregation*. All bare areas that are free from seed or other propagules, however, owe their pioneers to *migration* (Fig. 3). This includes all movements by means of which plants are carried away from the parent or their original home. The distance may be short, barely outside the area dominated by the parent, or very great, as in the case of wind-blown or water-carried germules. The fundamental process is moving the germules—seeds, spores, runners, etc.—away from the old and into the new area.

Migration alone, however, can not produce vegetation. It is entirely ineffective if the propagules do not grow. The seeds must germinate in the new area, the seedlings grow into mature plants, and these, in turn,

must reproduce if the area is to be vegetated. The migrants must make themselves at home, an idea that is expressed in the single term *ecesis*.

Ecesis sooner or later results in *competition*. The pioneer invaders may grow so far apart that no other plants encroach upon the same territory for water, nutrients, or light, or if they do there may be sufficient for all. In such cases, there is no competition. But when the plants are aggregated so that the demand for energy or materials is greater than the supply, competition begins. There is not enough for all; the stronger suppress the weaker; the latter are dwarfed or die as a result. Competition among plants goes on so quietly that it is usually unnoticed. Of 10,500 plants of the great ragweed (*Ambrosia trifida*) that germinated and started growth in a single square meter of rich, moist soil, only 192

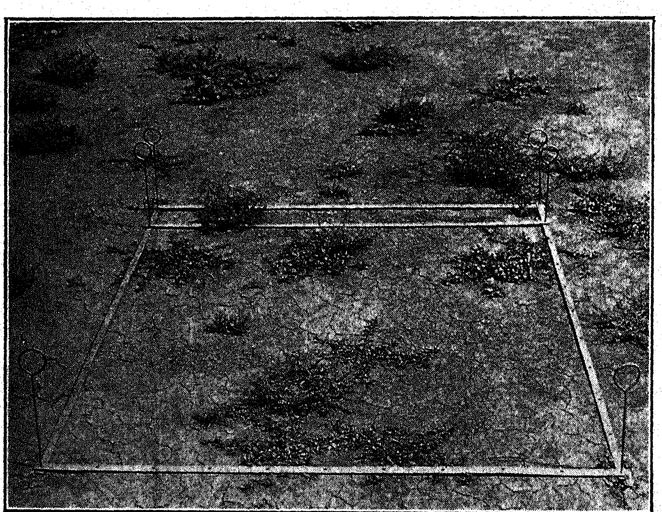

FIG. 3.—Migration of weedy annuals, knotgrass (*Polygonum*) and peppergrass (*Lepidium*) into a tennis court the surface of which had been covered with clay.

survived at the close of the season. All but 1.8 per cent died in consequence of insufficient light for making food. None of the survivors was fully developed, for on such a small area there was really only enough light available for the best growth of a few individuals.[560]

When plants grow together and compete for the necessary factors, they profoundly affect or react upon the place in which they grow. Competition results in *reactions*. The area once so fully lighted becomes more or less densely shaded. If it was wet, the large amount of water absorbed from the soil and lost through transpiration makes it drier. If it was dry, the accumulation of humus by the decay of dead roots, stems, and leaves adds to the water-retaining power of the soil. The dry area gradually becomes moister. The vegetation checks the wind movement near the soil where seedlings grow. Owing to the shade, temperature

becomes lower and less variable, and the air contains more water vapor than formerly, that is, it has a higher humidity. Moreover, the soil becomes richer, owing to the accumulated humus and the work of bacteria and fungi, and thus more favorable for plant growth.

The changes in the area are manifold. The vegetation has such a profound effect upon it that conditions for plant growth become very different. While early invaders may be unable to survive because of changed conditions and keen competition, others, which at first grew poorly or could not grow, now find the habitat favorable. Consequently, there is a shifting in the plant population as the developing vegetation

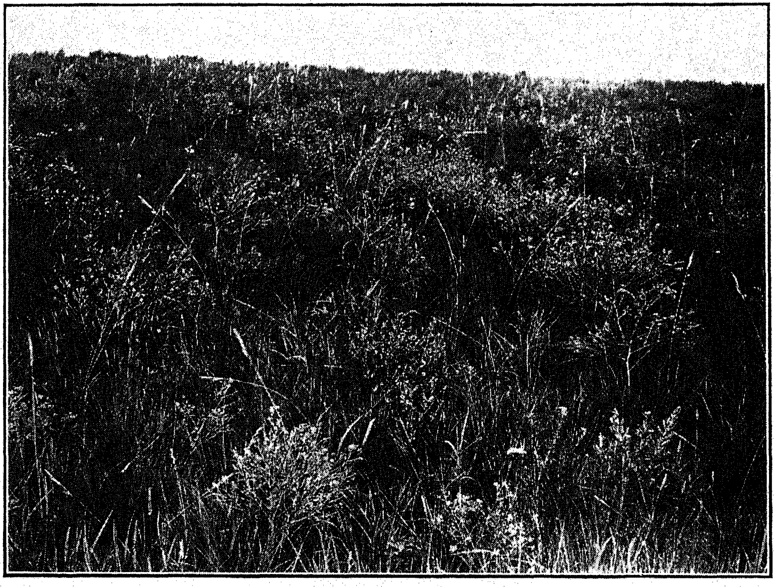

FIG. 4.—Grassland that has reached stabilization in eastern Nebraska on a soil similar to that in Fig. 3. Needle grass (*Stipa*) is the most important species; the bushy herb is the many-flowered psoralea.

modifies the environment. Shrubs may replace herbs in consequence of shading them, if conditions are favorable for their growth. Trees may be able to start under the shelter of the shrubs and, once fairly established, cause the disappearance of their benefactors. But whether herbs or shrubs or trees will be the final type of vegetation is determined by the climate, since the habitat can not be modified indefinitely.

If the precipitation is meager and evaporation high, only enough water may be present for the growth of drought-enduring grasses and their associates. Such is the climate of the plains. In western Washington and the mountains of Colorado, conditions are favorable for the growth of coniferous forest which is the final stage of development.

This is the highest type that the habitat can support under the present climate. The soil becomes no richer, the water content and humidity remain fairly constant, and light, also, is approximately the same. The vegetation is in equilibrium with its climate; it has become *stabilized* (Fig. 4). If it is cut or burned or the area otherwise partially or entirely denuded, the processes of migration, aggregation, ecesis, competition, and reaction, culminating in stabilization, are again repeated. Thus, like all organisms, vegetation arises, develops, matures, reproduces, and may finally die.

In cultivated vegetation, man is the chief agent causing migration. He also determines the density of aggregation and fosters ecesis. Moreover, the thoughtful grower of plants controls in a large measure the degree of competition by the rate of seeding and spacing or by thinning or transplanting. Since the reactions of the vegetation are modified by tillage and invaders largely kept down, stabilization is never reached.

How Vegetation Shows Structure.—Vegetation, like all organisms, not only undergoes development but also possesses structure. Much as higher plants may be divided into root, stem, leaf, flower, and fruit on the basis of structure and function, so vegetation may be divided into forest, grassland, chaparral, tundra, etc., on the basis of climatic control. Each of these is one of the larger units of vegetation called a *plant formation*. But no formation is uniform throughout its entire extent. Since the climate is different in various portions of the formation, differences in the vegetation occur.

A grassland climate dominates the region from the Missouri River through Nebraska, Kansas, and Colorado to the Rocky Mountains. Since precipitation, which is one of the most important climatic factors, decreases from 30 inches in the east to 15 inches westward, the tall-grass prairies in the region of higher rainfall give way westward to the vegetation of the short-grass plains. Such major divisions of the plant formation, *i.e. associations*, may be compared to the larger regions of stem or leaf such as epidermis, cortex, and stele.

Practically all vegetation shows more or less striking differences every few feet. Differences in the habitat—here a little drier, perhaps owing to thinner soil, there a little wetter because of a slight depression or greater humus accumulation—are reflected both in the number and in the kinds of plants. Where these differences are continuous, as around swamps or ponds, the structure of the vegetation is clearly shown in *zonation*. A belt or zone of floating plants in moderately deep water is surrounded by the tall, coarse, marsh vegetation of the pond margins, and this, in turn, may be bordered by sedge meadow. Forest margins usually exhibit definite zonation. The trees are bordered by a zone of shrubs and the latter, perhaps, by grassland (Fig. 5). Zonation may result from excessive salt accumulation in depressions. The center of

the area may be bare but bordered by zones of various halophytes (salt plants) in the sequence of their tolerance to alkali.

In any area of vegetation, usually only a little study is necessary to distinguish the controlling or *dominant species*. The others are either *subdominant* or *secondary*. In a mature forest of beech and hard maple, one may occasionally find a white pine or red oak, but these are present merely because the area is not completely occupied by the dominant beech and maple under the shade of which they can not grow. In more open forests such as yellow pine and bur oak, enough light penetrates through the dominant trees to permit a growth of shrubs and below these, in turn, grasses and herbs, while shade-enduring mosses and lichens occur

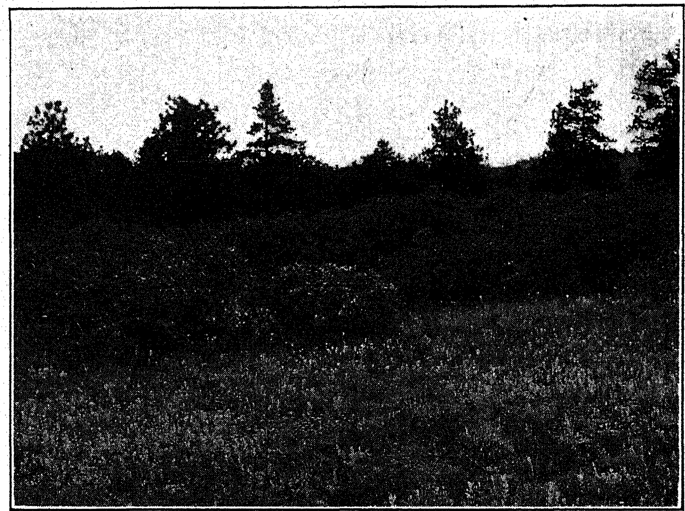

FIG. 5.—Zones of grassland, oak scrub, and yellow pine in Colorado.

on the forest floor. In fact, the presence and development of these species are controlled largely by the environmental conditions determined by the dominant trees. These various *layers* or vertical zones of plants are closely related to the decrease in light intensity from the primary layer of tree crowns downward. They are another expression of the structure of vegetation. Layering, although not so pronounced as in the forest, also occurs in grassland, and is characteristic of nearly all vegetation. It is revealed aboveground and among the roots as well. In cultivated vegetation it occurs when a nurse crop such as oats is sown with alfalfa or a cover crop in an orchard.

Where conditions change abruptly instead of gradually and zonation is disturbed or incomplete, vegetation exhibits *alternes*. This is illustrated where shrubs or trees extend up a moist north slope or ravine but do not occur on the drier areas. A series of parallel ridges may each

FIG. 6.—Alternation on north and south mountain slopes in Colorado. The north slope is covered with a stabilized forest of Douglas fir (*Pseudotsuga*), the south with oak scrub and scattered yellow pines.

FIG. 7.—Alternes of a short grass, buffalo grass (*Bulbilis*), in tall-grass prairie, due to overgrazing. Under natural conditions the former would soon disappear as a consequence of shading.

have one type of forest, *e.g.* yellow pine on the warm, dry, south slopes and spruce or fir on the cool, moist, north ones (Fig. 6). Moss-covered rocks or wet sedge lands in an otherwise forested area not only show abrupt differences in the structure of vegetation but also, like the undeveloped meristem in a mature root or stem, indicate an early stage in the development of that particular part. As time goes on, the meristem will become mature tissue, the rock will crumble to soil, the pond will be filled and, like the area occupied by the rock, will support the mature stabilized forest. Final development has merely been delayed (Fig. 7).

FIG. 8.—Society of daisy fleabane (*Erigeron ramosus*) in prairie late in June. It contributes a part to the summer aspect.

Vegetation shows structure not only in the general dominance, *i.e.* control of water, light, etc., by certain species, but also in local dominance at different seasons. In early spring in grassland, local areas are conspicuous because of the abundance and vigorous growth of certain herbs which blossom and mature seed. Such *societies* may make maximum demands upon the habitat before the grasses overtop them. By early summer, spring societies are inconspicuous and other societies of taller species are locally dominant (Fig. 8). The appearance of the vegetation again changes as summer gives way to fall. This adjustment of species to seasonal changes results in what are called *aspects*. It is another of the several ways in which vegetation shows structure.

CHAPTER II

METHODS OF STUDYING VEGETATION

Structure and development of vegetation and the manner in which these are affected by the factors of the environment should be studied with the same care and thoroughness as are individual plants. Vegetation readily responds to changes in the habitat. If the habitat becomes wetter or drier, better or more poorly lighted, etc., certain species and often whole groups of plants disappear and are replaced by others. Similar changes occur when vegetation is repeatedly mowed, grazed, burned, or cut as in lumbering. In the adjustment to a modified environment, the entire composition and structure of the vegetation may change. Such changes are not only of much scientific interest but are also frequently of great economic importance.

In range management, for example, it is important to know whether the most valuable forage species are able to reproduce and retain their place under the degree of grazing imposed upon them or are being replaced by less valuable ones. To be sure, this may be partially determined by superficial examination but usually not until the range has been depleted to such an extent that great loss in its grazing capacity has been incurred.[436] In reseeding overgrazed range or pasture land or in reforesting burned or cut-over areas, it is so important to know exactly how the herbaceous and tree seedlings are developing or to determine the cause of their failure, that exact methods of tracing the growth of the individual are in constant use.[433] The rate of increase or decrease in the number of poisonous plants on a range or the rapidity of distribution of introduced weeds in a pasture can be accurately determined only by careful study.

The Quadrat.—As the name indicates, the quadrat is a square area of varying size marked off for the purpose of detailed study (Fig. 3). It is one of the many unit areas that constitute the whole. Just as a knowledge of plant structure may be gained by examining in detail representative portions of the plant, so, too, by the study of numerous quadrats a knowledge of the structure of vegetation may be obtained. In its simplest form, the quadrat is used in counting the individuals of each species to determine their relative abundance and importance. It is also used to show exact differences in the composition and structure of vegetation. By its use, changes in the development of vegetation from season to season and from year to year may be followed and recorded in detail. Although a quadrat includes only a small area of vegetation, it

reveals the exact structure of this small part. It is impossible and, in fact, unnecessary to study the whole area of vegetation with the same thoroughness. A number of quadrats, located with care in places that appear different upon observation, will reveal the entire range of structure. The quadrat, like any other method, must be used with discrimination and it should be rarely located at random.

Kinds of Quadrats.—Quadrats vary in both size and use. The size varies from a square meter, which is used in grassland or most other herbaceous vegetation (*e.g.* cultivated fields of the smaller cereals, forest floor, etc.), to a square decimeter in studying soil-forming lichens and mosses on rocks. Areas of 100 square inches, each square inch marked off separately, are convenient in studying the development of seedlings (Fig. 88). In woodland when trees and shrubs alone are considered or in fields where the plants are large or rather widely spaced (*e.g.* maize, cotton, or sunflowers), a major quadrat, *i.e.* an area of 4, 16 or even 100 square meters, is employed.

Quadrats are also named with respect to their use. The *list quadrat* is one in which the species are listed and the number of individuals of each counted. *Chart quadrats* are those in which the position of each plant is accurately indicated upon the chart. *Permanent quadrats* may be of either kind, though they are nearly always charted. They are distinguished by the fact that they are marked in such a way as to permit of study from year to year. The *denuded quadrat* is a permanent one from which the vegetation has been removed in order that the manner in which the plants reenter may be followed. Frequently, the denudation is only partial, certain species only being removed or the aboveground parts of all the species at various intervals, by grazing, clipping, etc.

Marking Out Quadrats.—Cloth or steel tapes or strips of hardwood or strap iron slightly more than a meter in length and a centimeter wide are used in marking out quadrats. These are furnished with small holes or eyelets a decimeter apart and the ten intervals between the holes are numbered from left to right. They are held in position on the ground by means of sharp-pointed steel stakes with loops at one end (Fig. 3).

In marking out a quadrat, the far and near tapes are always so placed that the numbers read from left to right and the side ones so that they read toward the observer. Care must be taken to make the quadrat a square. In making a chart, a fifth tape is stretched across the quadrat parallel to the tape on the far side and a decimeter from it. The location of the plants in this decimeter strip is then indicated on the chart. The outside tape is moved to the next interval, enclosing another decimeter strip which is likewise charted, and so on, thus facilitating the rapid and accurate mapping of the whole quadrat (Fig. 9).

The List Quadrat.—This is used when it is desired to determine the kinds and abundance of plants. In listing a quadrat, *i.e.* counting the

number of individuals of each species, less conspicuous plants should be listed first as they are apt to be trampled. When the outside tapes and taller species afford sufficient landmarks, a single species is counted at a time. But if the vegetation is at all dense, a fifth tape is used to mark out each decimeter strip, and the plants are recorded as they are found. Except in cases of unusual difficulty, plants should never be broken or pulled as they are counted. Clusters and bunches of stems from the

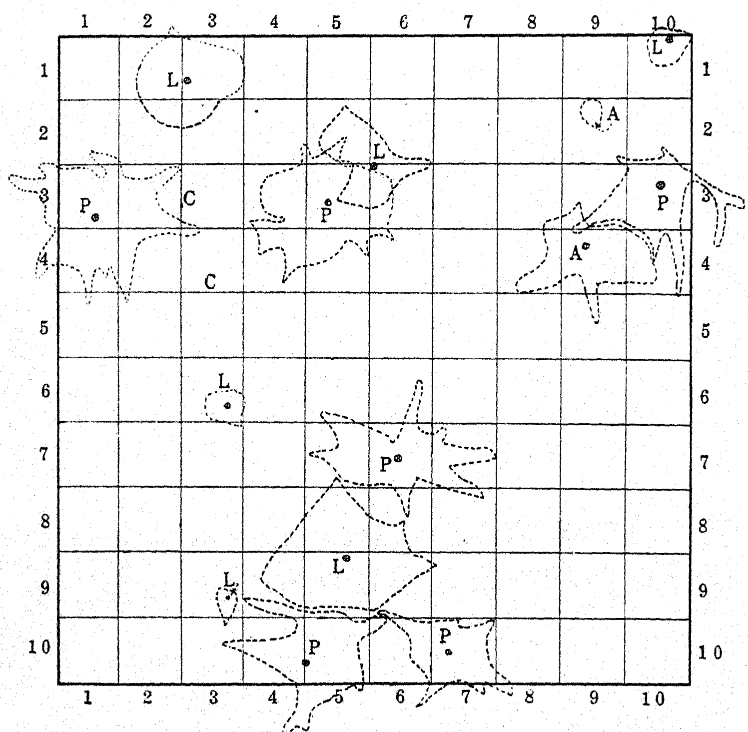

FIG. 9.—Chart quadrat of area shown in Fig. 3. *P*, knotgrass (*Polygonum aviculare*); *L*, peppergrass (*Lepidium virginicum*); *A*, prostrate amaranth (*Amaranthus blitoides*); *C*, green foxtail (*Chaetochloa viridis*). The dotted lines bound the areas occupied by the tops of the plants.

same root are counted as single plants. In the case of bunch grasses, each bunch is counted as one plant.

Making List Quadrats.—Select representative places in newly populated areas where the vegetation is not dense, such as weedy fields, gardens, or other disturbed areas. List all the species in the quadrats together with the number of each. Which species are annuals? Which ones have a longer life? Which is the most important and which is the least important species? Make a list of the kinds and numbers of weeds in the quadrats in a pasture. If possible, list the same quadrats again in spring or fall.

This listing of the species in various parts of the area gives definite information as to the composition of the vegetation.[402] Not only does this reveal the kinds of plants that occur in a habitat but also, what is quite as important, the species the habitat does not support. Moreover, a definite idea of the relative number, size, and, perhaps, duration of the various components is gained. Such careful examination of selected areas will permit a close estimate of the extent of unoccupied soil. A few list quadrats on north and south slopes or on the crests and lower slopes of hills will reveal marked differences in the vegetation and often permit a preliminary grouping of plants upon the basis of differences in the habitat, especially the water content.

Data from 70 list quadrats on exposed south and southwest and sheltered north and northeast slopes in the prairie of eastern Washington revealed the fact that on the southerly slopes only 112 individuals occurred per square meter, where approximately 19 per cent of the soil surface was bare, while the northerly slopes, with only 3 per cent bare soil, supported 200 plants in a unit area. Furthermore, it was found that while certain species of grasses, the dominants, were rather equally distributed on both slopes, the subdominants showed a preference for either the one or the other and some were confined almost or entirely to the north or south hillsides. The differences in distribution were shown to be due to differences in the habitat, a much greater water content and humidity prevailing on the northerly slopes.[558]

In grazing studies, list quadrats are often permanently located in pastures and also in areas protected from grazing. Usually, a record is kept from year to year of only the more important species. In North Dakota, it has been shown that while certain of the best grasses almost entirely disappeared under close grazing, weedy herbs, such as certain sages, which are not eaten at all or only when the other vegetation is very sparse, were greatly increased. At the end of 5 years, they were five times as abundant as in ungrazed or normally grazed areas where they were held in check by the grasses. Not only had they increased in number but also in size and they soon became so abundant that the value of the pasture was greatly reduced.[443]

The principle of the list quadrat is employed in estimating crop yields. In the case of the smaller cereals, the average number of plants per square yard is determined; next, the number of stalks bearing spikes; then the number of spikelets; and, finally, the number of kernels in spikelets of average size. Such determinations in several places in the field permit forecasting the yield with exceptional accuracy. Studies on the percentage of germination, rate of tillering under different conditions of soil, applications of fertilizers, etc., are accurately made by means of the list quadrat. Similar methods may be used in studies of the eradication or control of weeds including poisonous plants such as loco weeds (species

of *Astragalus* and *Aragallus*), larkspurs (*Delphinium*), death camas (*Zygadenus*), etc., on western ranges. The list quadrat is also regularly used in making disease surveys which deal with the number of rust-infected plants or smutted heads of the cereals.

The Chart Quadrat.—The chart quadrat is employed when a more detailed record of vegetation is required. The position of each plant within the square meter and the areas occupied by bunches, mats, or

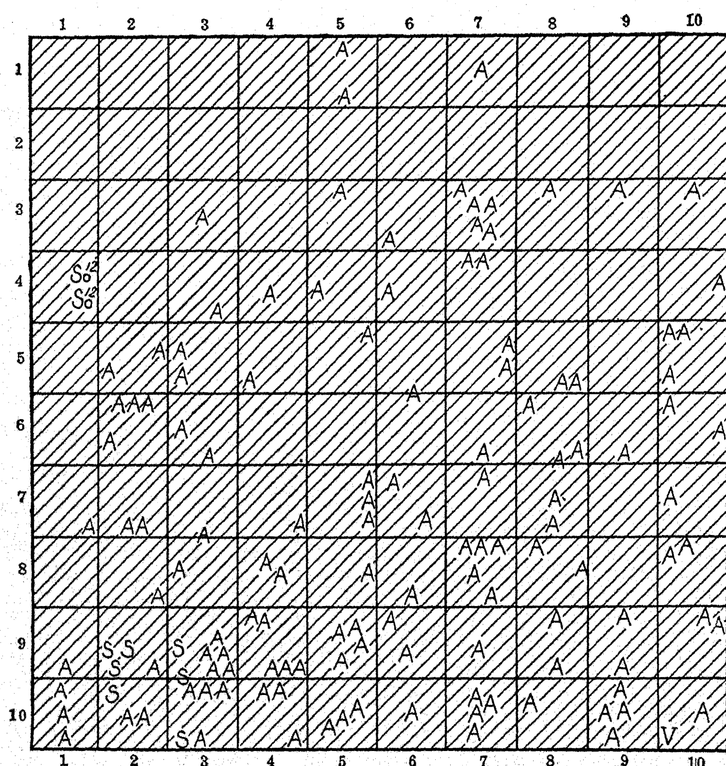

FIG. 10.—Quadrat in an overgrazed pasture near Lincoln, Nebraska, where the tall grasses have largely been replaced by buffalo grass. Charted June 11, 1924, of the first season of protection from grazing. Left hatch (*Bulbilis dactyloides*); *A*, wheat grass (*Agropyron smithii*); *S*, dropseed (*Sporobolus asper*); *So*, wolfberry (*Symphoricarpos occidentalis*), the exponent being the height in inches; *V*, speedwell (*Veronica peregrina*).

turfs of grasses, mosses, etc., are determined and recorded upon a chart. This forms at once a record of the present structure and a basis for determining future changes.

The vegetation is mapped on coordinate paper, a square decimeter in size, to a scale of 1:10. Where the vegetation is dense, consisting of a great number of individuals in a small area, a larger scale is often more convenient, one of 1:5 usually being sufficiently large. The chart is

made on paper ruled to square centimeters and each square decimeter of vegetation occupies 4 square centimeters on the chart. In making quadrats of forest trees, the scale is 1:100 or 1:500. In this case, the chart remains the same size but it represents a greater area.[110,326]

Mapping is begun at the farther left-hand corner of the chart after the fifth tape has been fastened in place. The plants in the first square decimeter of the quadrat are indicated in their relative positions in the first square centimeter on the chart. Individual plants are indicated by a single letter, usually that beginning the generic name, except where two or more begin with the same letter in which case two letters may be used (Fig. 10). The number of stems from one root is indicated by an exponent with the proper initial unless the stalks are far apart. The areas occupied by turfs, mats, or bunches of grass, mosses, and large rosettes are outlined and may be indicated by hatch work. When the first decimeter strip is completed, the upper tape is moved to enclose a new decimeter strip, and this is repeated until the quadrat is finished. It is sometimes desirable to start with the bottom row and work upward, thus avoiding injury to the plants by stepping or lying on them before they are charted. This is especially necessary in working with dense vegetation. If a photograph of the quadrat is to be made, this should be done before the vegetation is disturbed.

Making a Chart Quadrat.—Select an area where the plants are rather widely spaced and chart a square meter of the vegetation. After the method is learned, typical meter quadrats of grassland, forest herbs, and woody seedlings or offshoots, etc., and major quadrats of forest trees should be plotted. In the latter, indicate the diameter of the trees by an exponent following the initial. Write a concise statement as to what information each quadrat gives about the vegetation of the particular area in which it was made, and draw comparisons between the various communities.

Certain modifications of the chart method are often desirable depending upon the object to be attained. Sometimes it is sufficient to determine the area occupied by the more important forage species only. In such cases, bunches or mats of the two or three dominants are charted without reference to subdominants. This may usually be done in only a fraction of the time necessary for making a complete chart. Similar studies in the management of certain forest types such as reproduction of aspen from roots and stumps may be followed with little reference to herbaceous vegetation.[435]

The pantograph is an instrument frequently used in charting quadrats. It is especially valuable in accurately reproducing the outlines of mats and tufts of vegetation and in locating individual plants where vegetation is not too dense. The operator guides a pointer about the periphery of tufts and bunches, etc., and their size is automatically reduced to one-fifth and recorded in exact position upon the record sheet.[237]

Undoubtedly, the desirability of studying the same area at different times during the season or from season to season has already occurred to the reader. This may be readily accomplished by means of the permanent quadrat.

Permanent Quadrats.—Quadrats may be made permanent by marking precisely the position of the original ones. This should be done very carefully by means of placing stakes at the intersections of the tapes in

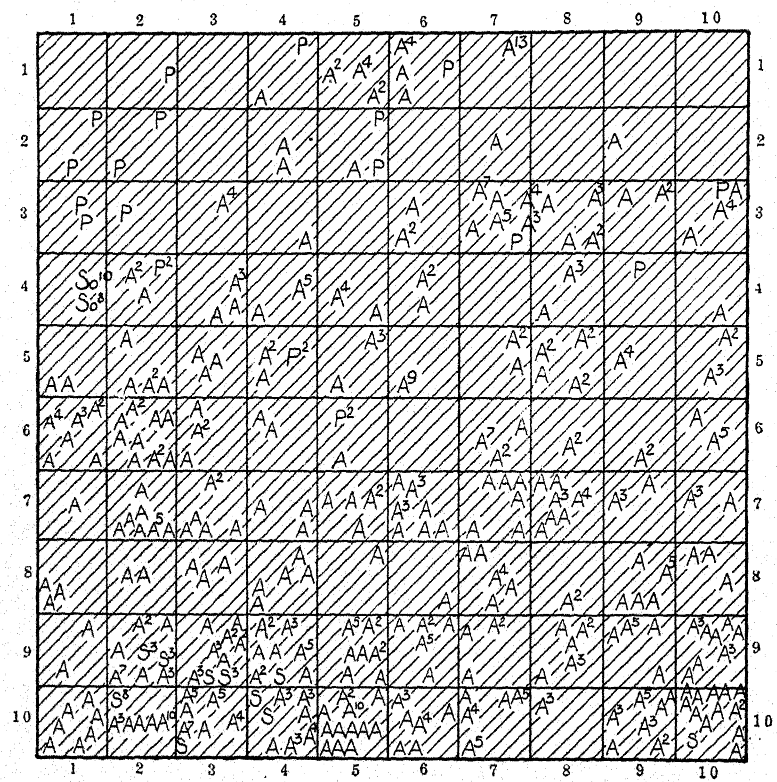

Fig. 11A.

the upper left- and lower right-hand corners. Since wooden stakes are not permanent and may be easily destroyed, metallic pegs about 12 inches long and an inch or less in diameter may be securely driven into the ground so that they scarcely protrude, and if the ends are blunt, domesticated animals will not be injured should they chance to step on them. A taller wooden stake, just outside the iron one where the mapping is started, will help in relocating the area. It should be definitely located with reference to natural or artificial landmarks in order that it may be easily found upon successive visits.

Permanent quadrats may yield much information even in a single year and often in a few weeks (Fig. 11). For example, counting and relisting the species in any waste area in spring will usually reveal marked changes in short periods of time. Permanent quadrats in grassland or forest show striking changes as the season progresses. One group of species will become conspicuous because of the flowers and fruits and will then give way to another, which, in turn, reaches its height of activity

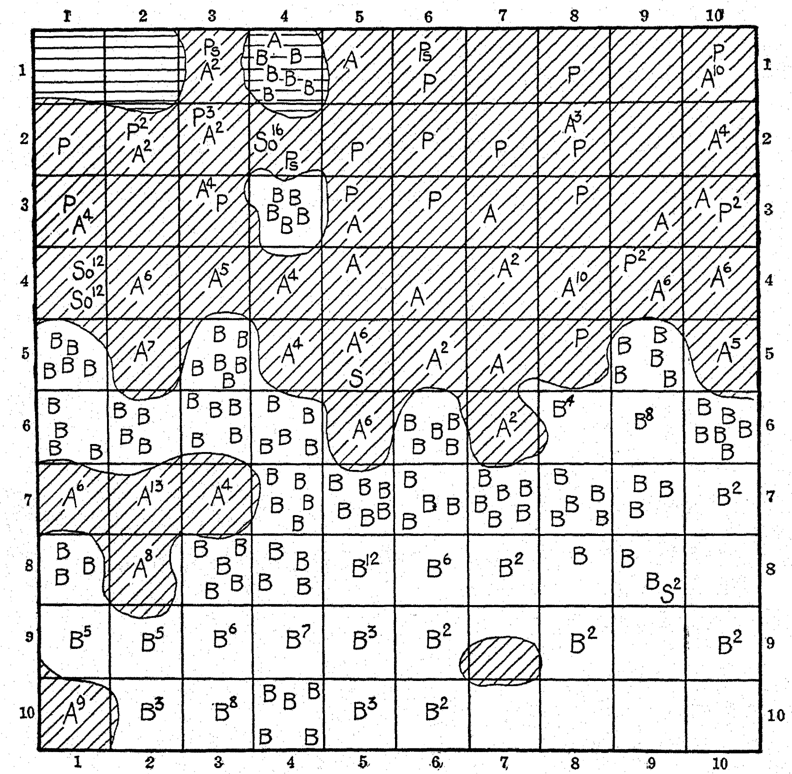

FIG. 11B.

FIG. 11.—Quadrats as in Fig. 10. The first was charted on May 29, 1925, and the other on June 4, 1926. Left hatch or *B* (*Bulbilis dactyloides*), the exponent indicates the number of stems or unit clumps; *A* or unhatched area, wheat grass (*Agropyron smithii*); horizontal hatch or *P*, bluegrass (*Poa pratensis*); *Ps*, panic grass (*Panicum scribnerianum*); rest of legend as in Fig. 10.

What was the dominant species in 1924? Count the number of wheat grass stems in the three lower rows of quadrats 1 (Fig. 10) and 2, and calculate the percentage increase under protection. Determine the percentage increase in the rest of the quadrat. Compare the percentage of the area dominated by buffalo grass in 1924 and 1926. From how many of the unit areas has buffalo grass been shaded out? Is it losing its hold elsewhere? Are any of the other species of importance? Has the wheat grass increased its abundance in the four upper decimeter rows during the 3 years? Will the future vegetation in this quadrat be tall grass or short grass?

and wanes and is then replaced in importance by still another. By the use of the permanent quadrat, a complete record of the *prevernal* (early spring), *vernal* (spring), *estival* (summer), and *autumnal aspects* of vegeta-

tion is secured. Species in flower or fruit are indicated by a horizontal line through the symbol, while a vertical line indicates a seedling.

Permanent quadrats recharted year after year in originally bare areas give the complete story of development. The fate of seedlings, the time required for the survivors to mature and produce seed, the method, rate, and success of vegetative propagation, as well as the length of life of the individual, make an interesting story. One can see how the plants have aggregated; follow the invasions of new migrants; trace ecesis; gain much information about competition and how it results in the appearance of new species and the disappearance of others; with proper instruments, determine the changed conditions within the habitat resulting from reactions of the developing vegetation; and finally, discover how it all ends in stabilization. Permanent quadrats in the path of retreating glaciers in Alaska are yielding much data on all these processes and should reveal much of the history of glaciated parts of those states that were once covered by the ice sheets.[113]

Quadrats in such dynamic areas as sand dunes, river bars, or flood plains, or on the border line or *ecotone* between two plant communities, such as shrub and grassland, often show remarkably rapid changes, and many of the principles of ecology are illustrated by a comparison and interpretation of the charts from permanent quadrats.

The importance of a knowledge of the life history of the individual, under what conditions the seed will germinate and the seedling become established, can not be overemphasized. Forests are composed of individual trees and ranges of species of grasses and other herbs, all of which must germinate, grow, mature, and reproduce unless vegetation is to disappear. By studying these communities and the way in which they are affected by various degrees and types of grazing, a system of management has been worked out for native grazing lands. By means of this system they have been fully revegetated and the range maintained at a high state of production without the loss of the forage crop for a single year or the presence of a forest-fire risk as a result of the nonremoval of the herbaceous vegetation.[432]

Results in reforestation are scarcely less marked. An exact record of the fate of the tree seedlings, losses due to rodents, winterkilling, frost heaving, damping-off, etc., can be had only by a detailed study of representative areas. Changes in the development of the herbaceous and shrubby vegetation by which one group of plants replaces another, a process called *plant succession*, and the effects of this on the tree seedlings are studied in detail. Such knowledge is indispensable in the proper management of the forest.[384]

A Study of Permanent Quadrats.—Select and permanently mark out quadrats in one or more of the places suggested in the preceding paragraphs, or very carefully rechart permanent quadrats where the previous composition of the vegetation has

been recorded. These should be visited and recharted once or more each year, the several charts studied and compared, and explanations suggested for the changes that have taken place.

The Denuded Quadrat.—It is frequently desirable to remove the vegetation by cutting, grazing, burning, or flooding or by a more profound disturbance such as removing the surface soil with its roots, rhizomes, seeds, etc. The permanent quadrat thus becomes a denuded one. In partially denuded quadrats, only certain species are removed or a portion of the area denuded.[98]

In experimental pastures, clipped quadrats are used in which the vegetation is cut close to the ground (Figs. 12 and 13). On the prairies

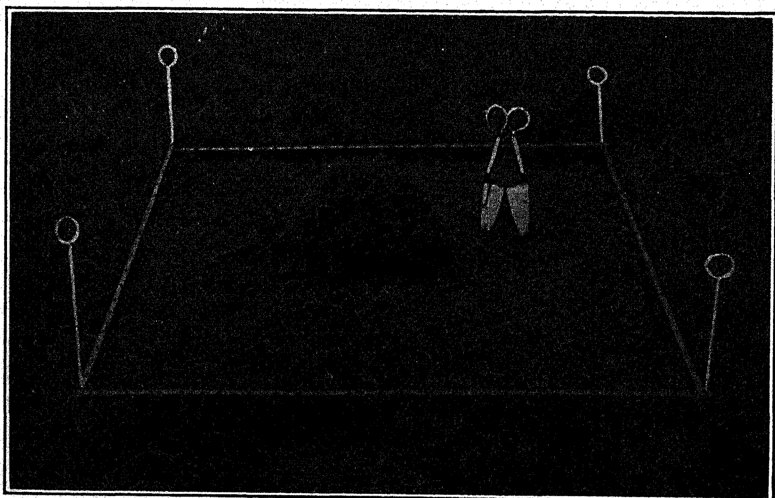

FIG. 12.—Clipped quadrat in the short-grass plains of eastern Colorado.

of North Dakota, for example, this method was employed to determine the most active period of growth of the different species and the effect upon growth of the frequent removal of the vegetation as in close grazing. At each clipping the vegetation was weighed and the proportional weight afforded by each of the more important species was determined. It was found that four species produced approximately half of the forage and that, among these, blue grama (*Bouteloua gracilis*) produced a fairly uniform growth throughout the year. Needle grass (*Stipa comata*), like most of the others, gave a light yield toward the close of the season. Two species of sedges (*Carex*) produced the most abundant growth very early in the spring, but the yield rapidly became less with the oncoming of summer. Needle grass disappeared in direct relation to the frequency of clipping, but the growth of grama grass and sedges was stimulated by moderate clipping, persisting, although in a much weakened

condition, in quadrats where practically all the other vegetation had disappeared.[443]

By the use of similar methods, it has been found that the ranges of the Southwest are seriously depleted by prairie dogs, which not only eat the same kinds of grasses as the cattle and in the same order of preference but also in large quantities.[523]

The most important objects sought in the revegetation of native pastures are a continuous, vigorous growth and ample seed production. Clipped and grazed quadrat studies in the Blue Mountains of Oregon and the Wasatch Mountains of Utah have shown that the removal of the herbage several times in a season, especially if the first harvest is made a few days after growth has started, seriously weakens the plants and immediately decreases their forage production. For example, plots

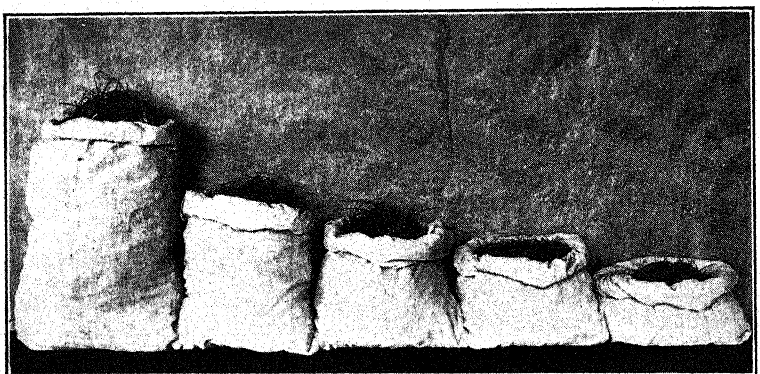

FIG. 13.—Average decrease in the production of natural vegetation per square meter, proceeding westward from eastern Nebraska to eastern Colorado.

harvested once each season just before seed maturity yielded more than five times as much forage as those from which the vegetation had been removed four times during the year. Moreover, plants in the latter quadrats became so weakened from starvation that they failed to produce flower stalks and viable seeds.[432] The applications of these results to grazing practice are evident[438] (Fig. 14).

The practice of burning pastures and ranges to make fresh feed available earlier in the spring and to get rid of old vegetation on areas so lightly grazed during the previous season that there is danger of uneven grazing has been investigated in Kansas by denuding quadrats by burning. After 4 years of late winter burning, the grasses had increased 21 per cent in density, other herbs had decreased in abundance, and vegetation began growth earlier in the spring.[234] These results, however, are not in complete agreement with those obtained in drier regions where burning is almost as destructive to the grasses of the range as it is to the trees of the forest.[437] Burning of bluegrass pastures has also been found

to be harmful.[195] The effects of forest fires, burning brush land, disposal of slash after lumbering as well as the growth of subsequent vegetation upon the reproduction of the forest are all studied with a high degree of accuracy by the quadrat method.[324]

The complete sequence of the developmental stages from bare area to stabilized vegetation may be secured if a few quadrats are denuded each year. These should be located in a series with intervening stabilized vegetation. Thus, a time sequence is established and the different stages closely brought together for study. Naturally, differences in small, bare areas are not so extreme as in larger ones and they will, therefore, be more quickly revegetated, in part because of the nearness of plant propagules. Such areas, whether in forest, swamp, scrub land, desert, or prairie, offer excellent opportunity for study. Since denuding practically makes a new habitat, the change of factors (light, water content, etc.) should be measured and compared with those of the adjacent undisturbed quadrats. The vegetation in the latter also serves as a control.

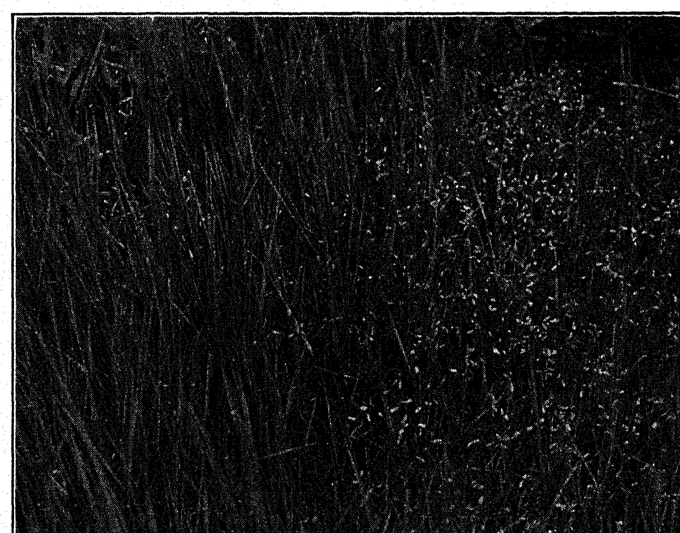

FIG. 14.—Development of wheat grass and disappearance of buffalo grass (left) after 3 years of protection from grazing, and persistence of buffalo grass (right) where the cattle have reached over the fence and grazed.

Transects.—It is frequently desirable to know just how vegetation varies with changing environment, such as is caused by slope exposure or other irregularities in topography or soil, or to determine how one community of plants gives way to another. This may best be ascertained by a transect, which is a continuous narrow strip that gives a cross-section of the vegetation. Transects are indispensable in studying

zones, alternes, and transitions of all kinds. They are always made at right angles to the extension of the zones or ecotones.

Line Transect.—The simplest form of transect and one that is most easily charted is the line transect. It is employed when only the more striking differences in structure are sought. It is made by running a measuring tape, of considerable length and marked off like a quadrat tape, along a selected line. The position of the individual plants touching the tape on one or both sides is recorded on a line on the chart drawn to scale (Fig. 15). As in the quadrat chart, the scale employed varies with the type of vegetation, but it should always be large enough to prevent crowding. In noting the plants that occur along the tape, every second vertical line on the centimeter plotting paper is taken to correspond with the tape. The plant that touches the latter is recorded to the right or left, respectively, and within the centimeter square that corresponds to the particular decimeter interval of the tape. When it is desirable to save time, plants are noted only on one side. The species are indicated by initials as in quadrat mapping. Thus, a record is obtained of the position of individual plants, the space between them, and the relative numbers of individuals of the different species met along the transect line.

In plotting, the topography is carefully drawn to scale. If it is not level, it is necessary to obtain the length and angle of each slope in order that an exact profile map may be constructed. The rows of initials are then transferred from the field record to the outline, centimeter by centimeter. A 5-meter transect can thus be recorded upon a meter sheet on the scale of 10:1. By use of the line transect, a considerable area may be sampled in a relatively short time and the topographic features noted. Differences in the structure of vegetation are thus clearly shown.

Belt Transect.—The belt transect is a strip of vegetation of uniform width and of considerable length. The width is determined largely by the character of the vegetation, just enough being included to reveal its true structure. In herbaceous vegetation, the usual width is 1 decimeter, but it varies from 1 to 10 meters in woodland. The 1-meter transect is employed if the shrubs and seedlings of the forest floor are included, but if mature trees only are mapped, the 10-meter transect is best. The length of the transect is determined by its purpose. It may be made permanent by marking with a stake at each end. Since this transect includes width, it permits of a more detailed and accurate record of the arrangements of plants. In staking a belt transect, two tapes are employed to mark out the strip of desired width. The distance between them is uniform throughout and they are held in place by quadrat stakes. The plants are recorded as for the chart quadrat, except that an interval of a centimeter is left between the successive portions of the strip in order that they may be cut and pasted or readily copied

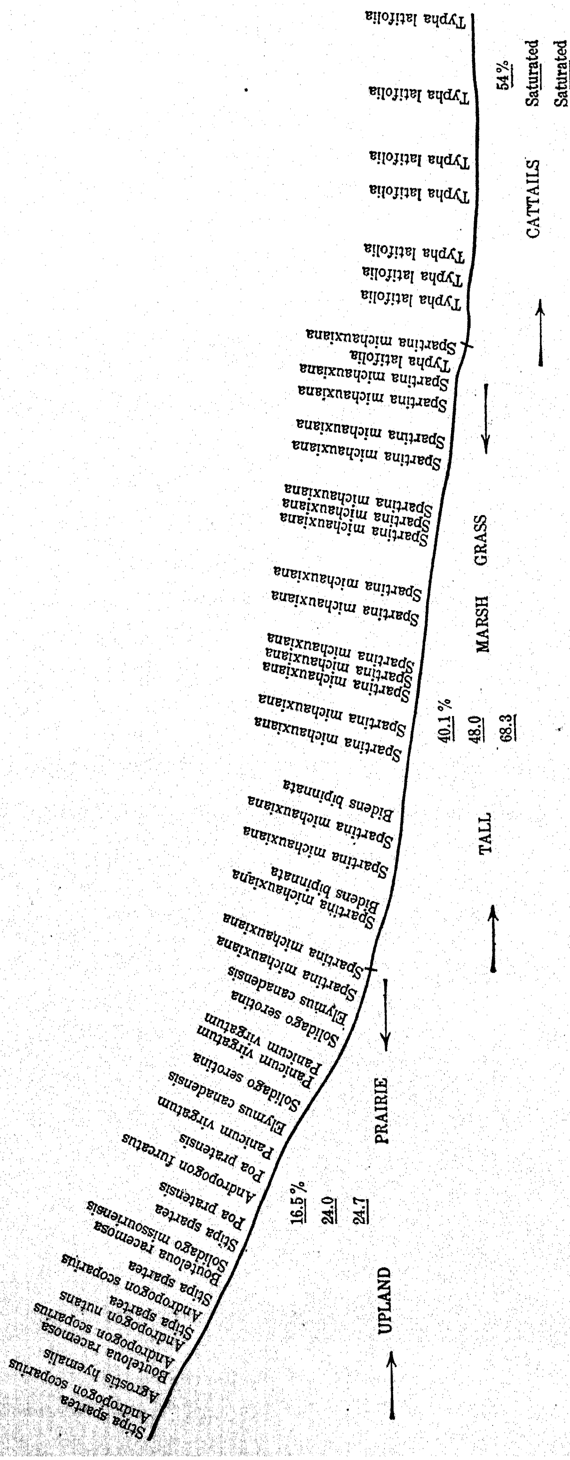

FIG. 15.—A line transect 5 meters long extending from upland prairie through tall marsh grass into a cattail swamp. The relative water content in the three communities is also shown at depths of 0 to 6, 6 to 12, and 12 to 24 inches, respectively.

on the topographic outline. The latter is traced on the plotting paper as indicated for the line transect, except that it consists of two parallel lines instead of one.

The belt transect shows a definite range of vegetation and by making it permanent and recharting at suitable intervals, changes in the vegetation along the line of the transect may be readily detected and measured. The factors causing the differences in the plant cover should also be determined wherever possible. The limits of zones may be shown on charts of belt transects by single cross-lines. For example, the boundaries between upland prairie and tall marsh grass and between the latter and cattail swamp were definitely fixed (Fig. 15). In the course of only 6 years, owing to a gradual building up of the ravine and consequent better drainage, the cattails had entirely disappeared and their territory had become occupied by tall marsh grass. Moreover, the upland grasses extended farther into the former marsh-grass zone.

Portions of a transect in the prairie of eastern Nebraska extending from the top of a gravelly hill to its lower slope are shown in Fig. 16. Because of differences in soil and slope exposure, marked differences in vegetation occur. The grama grass

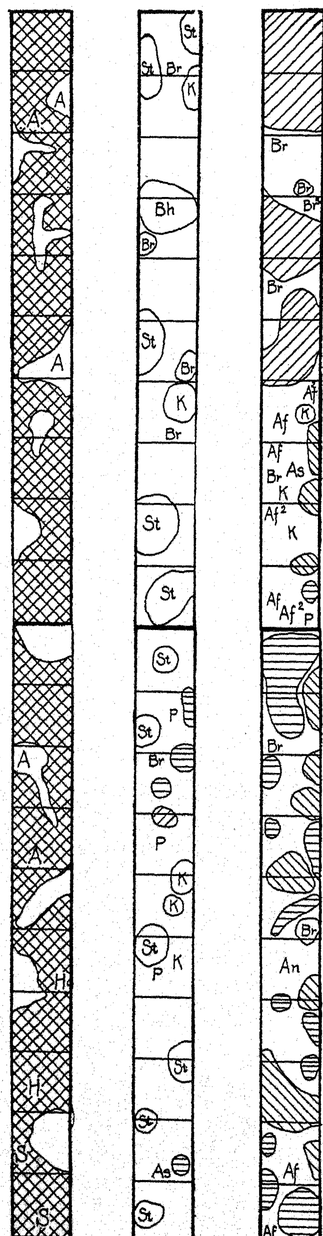

FIG. 16.—Portions of a transect 1 decimeter wide (each 2 meters long) from the top of a steep hill (left), from its southeast slope (center), and from its base (right). The gravelly loam at the top, with a water content of 5 to 18 per cent, is dominated by blue grama (*Bouteloua gracilis*), also common on the Great Plains. The sandy loam half way down the slope, water content 13 to 30 per cent, is dominated by needle grass (*Stipa*) and June grass (*Kœleria*), both characteristic of upland prairie. The silt loam soil at the foot of the slope and only 200 feet from the hilltop, with a water content of 17 to 40 per cent, is dominated by the bluestems (*Andropogon*) which require more water. *A*, western ragweed (*Ambrosia psilostachya*); cross-hatch, blue grama (*Bouteloua gracilis*); *H*, sunflower (*Helianthus rigidus*); *S*, dropseed (*Sporobolus asper*); *St*, needle grass (*Stipa spartea*); *Br*, slender grama (*Bouteloua racemosa*); *K*, June grass (*Kœleria cristata*); *Bh*, hairy grama (*Bouteloua hirsuta*); parallel hatch or *P*, Kentucky bluegrass (*Poa pratensis*); right hatch or *As*, little bluestem (*Andropogon scoparius*); left hatch or *Af*, big bluestem (*Andropogon furcatus*); *An*, Indian grass (*Andropogon nutans*).

on the crest is the same species that is so abundant in the dry, short-grass plains; the tall bunch grasses on the upper slope indicate a less arid situation and, like the lower portion dominated by bluestems, are typical of great expanses of grassland in eastern Nebraska, Kansas, and Dakota.

A transect 10 meters wide running northward from the crest to the foot of a slope and over a hill in the deciduous forest of eastern Nebraska is shown in Fig. 17. At intervals of 8 meters, cross-tapes were inserted and in the areas thus delimited each tree was charted in its relative position and its diameter taken at a height of 3 feet. By a study of the results thus obtained (which are summarized in the figure) it was fairly easy to delimit the plant communities. Measurements of water content throughout the season showed that the bur oak-yellow oak community was always driest and the others pro-

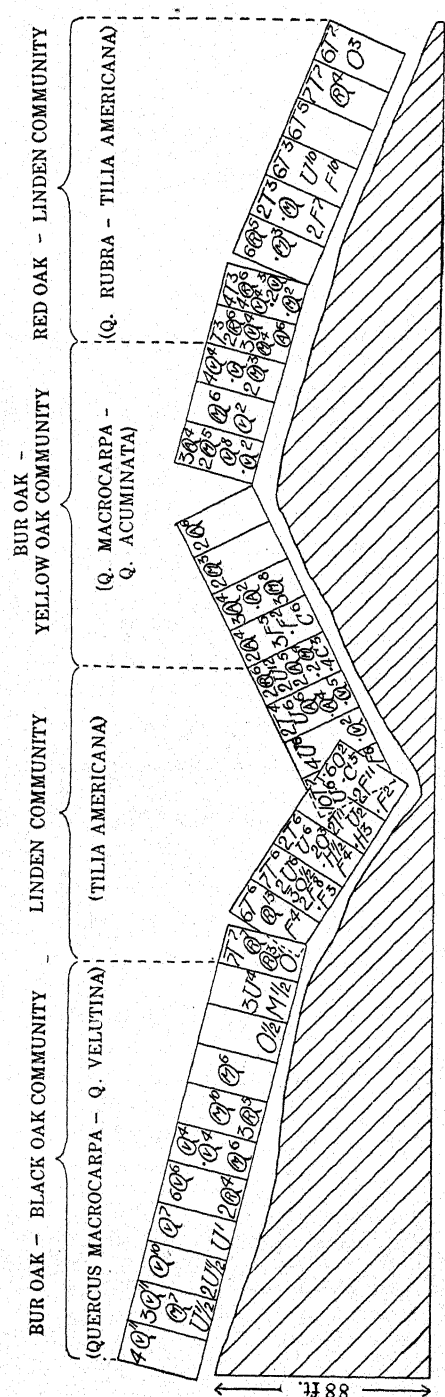

FIG. 17.—A belt transect 10 meters wide and 280 meters long.

QM Bur oak (*Quercus macrocarpa*) **QR** Red oak (*Q. rubra*) *O* Ironwood (*Ostrya virginiana*) *M* Red mulberry (*Morus rubra*)
QA Yellow oak (*Q. acuminata*) *T* Linden (*Tilia americana*) *F* Green ash (*Fraxinus lanceolata*) *H* Bitternut hickory (*Hicoria minima*)
QV Black oak (*Q. velutina*) *U* Red elm (*Ulmus americana*) *C* Redbud (*Cercis canadensis*) . before a letter indicates the tree is dead.

What oaks occupy the drier slopes and hilltops? The lower, moister areas? The linden requires the most moisture and, like the red oak, the seedlings can grow in deep shade. All of the other trees would grow best, too, on the lower slopes but they can not endure the shade of the red oak and linden. In what community do most of the dead trees occur? Are they large trees? What was the probable cause of their death? Do any bur oaks occur in the red oak or linden communities? Do any lindens occur in the bur oak-yellow oak or bur oak-black oak communities?

gressively more moist toward the bottom of the slope. Humidity was also least near the hilltop, but the light was strongest.[400]

Transects are used in determining the influence of trees upon other plants, especially as affected through water content and light. About the roots of yellow pines in Arizona, for example, the soil is drier and the vegetation much sparser than in soil where roots are not present. Conditions for reforestation are thus modified within a radius of 30 to 40 feet from the trees and even beyond the zone of root activity.[384] Transects several meters wide, extending from windbreaks composed of rows of trees into fields of cereals, alfalfa, and other crops, reveal a decreased production in the area of root competition and shade. If the transect is extended still farther, however, the beneficial effects of the windbreak are usually shown in the yield being increased to an amount that more than compensates for the loss near the trees.[20]

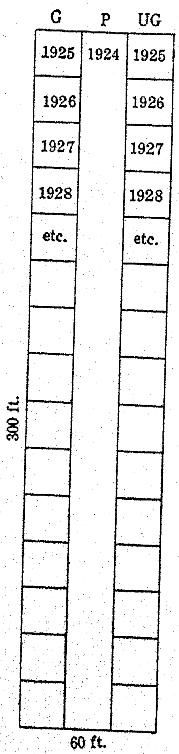

FIG. 18.—Isolation transect consisting of a series of units *G* closed from grazing on the years indicated; a protected, ungrazed strip *P*; and a series of ungrazed units *UG*, some of which were opened for grazing on the years indicated.

Isolation transects are regularly used in grazing experiments. These consist of two strips, each 300 feet long and 20 feet wide with a protected strip between as a control (Fig. 18). One is grazed, the other ungrazed. At the end of each year one 20-foot square unit of ungrazed area is opened and one of the grazed units closed. Thus, after a few years, a history of the development of vegetation as affected by 1, 2, 3, or more years of grazing may be seen as well as its development after 1 or more years under protection.

The belt-transect method has been used very successfully for recording the composition of tropical rain-forest and especially for commercially important trees. The belts are of sufficient width (66 feet) and frequency (1.25 miles apart) to include 1 per cent of the area.[166] In fact, the method has long been used by American foresters, although they make an optical estimate of the width of the area cruised and record the number and size of merchantable trees instead of mapping them.[571]

Making Transects.—Make a line transect 3 to 5 meters long at right angles to the zones about a pond or including the transition area (ecotone) between two different communities such as scrub and woodland, etc. Locate areas where the vegetation changes abruptly due to differences in slope, depth of soil, grazing, burning, or for other causes, and mark out and plot a belt transect of appropriate length and width. Belt transects 5 to 10 meters wide and including only the trees should be plotted from the top of a forested, steep hill or bluff to a flood plain below, including a part of the latter. Point out the differences

shown by the transect, indicate the dominants in each area, and suggest reasons for the changes in structure.

The Bisect.—The structure of vegetation with regard to the relative height and lateral spread of plants and the interrelation of one plant to the other is important. It is equally essential to understand the relative position, depth, and extent of underground parts. Such information may be gained by the use of the bisect. It is essentially a line transect along which a trench has been dug to a depth greater than that of the deepest root systems. The underground parts such as rhizomes, corms, etc., as well as the roots of each plant, are isolated and the position and extent of each carefully measured and plotted to scale on coordinate paper. The whole root system, so far as it can be represented in one plane, may be drawn, but if the vegetation is at all dense, only that part occurring in the first 4 inches of the trench wall need be represented. This method reveals the form of the root systems of different species and shows their relationships to each other and to different layers of soil, etc. Without an exact knowledge of these facts, an understanding of the structure and economy of a plant community is incomplete. While the line transect shows the structure of vegetation in one dimension and the belt transect in two, the bisect supplements these by showing the third.[561] (Fig. 19.)

It is often unnecessary to chart the root system of every species. Frequently the dominants alone will suffice. It is best to measure and draw or photograph the shoots to scale first, for they are often more or less disturbed while excavating the parts underground. The work of making a bisect chart is usually lengthy and laborious and especially so where deep-root systems are involved, but the results obtained fully warrant its use. A few examples will best reveal its value.

On the Great Plains, under 17 inches annual rainfall, great differences in the type of vegetation are found on level lands within a radius of a few miles. Certain areas are covered with the short, buffalo (*Bulbilis*) and grama (*Bouteloua*) grasses, others with tall bunches of bluestem (*Andropogon*) and other herbaceous vegetation, while certain areas are characterized by extensive growths of wire grass (*Aristida*), a species of intermediate height. Bisects revealed the fact that the short grasses grow in silt loam so compact that surface run-off frequently causes the loss of over one-third of the precipitation. Usually, the surface 12 to 18 inches of soil alone are moist and absorption by grass roots is largely confined to this layer. But in the sandy soil where the bluestem grows, practically all of the rainfall is absorbed, the soil is moist to depths of 4 to 5 feet, and to this depth it is ramified by the deep roots of the tall grasses and other herbs. In the semi-sandy wire-grass areas, water penetration and root depth are intermediate. Thus, the causes underlying the distribution of the three communities were clearly revealed

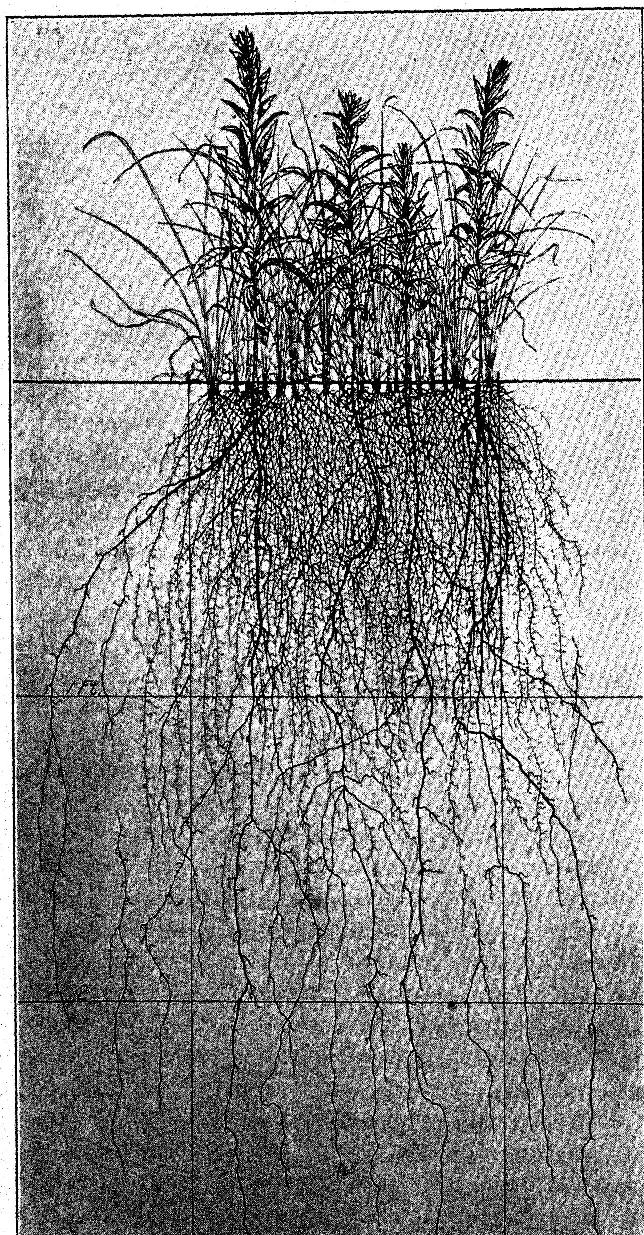

Fig. 19.—Bisect in prairie showing root and shoot relations of the little bluestem (*Andropogon scoparius*) and prairie false boneset (*Kuhnia glutinosa*) at the end of the first summer's growth.

and much information made available for an intelligent understanding of the behavior of crop plants when grown in these areas.[461]

Bisects have been made in fields of the smaller cereals in loam soils from the Missouri River to the Rocky Mountains and in three grassland communities. Westward, with decreasing rainfall, the plants are much shorter and the roots decrease in length from about 7 feet to approximately 2 feet. The plants, moreover, show a strong tendency to grow in clumps or bunches, in this respect resembling some of the native grasses which form a sod in moist situations but grow in bunches in dry places.[562]

Vegetation in the Wasatch Mountains develops from a mixed grass and weed stage, dominated by needle grass (*Stipa*) and yellowbrush (*Chrysothamnus*), into a growth of the sod-forming wheat grasses (*Agropyron*). Why the yellowbrush gives way to the wheat grass is clearly revealed by the bisect. The dense sod formed by the roots and rhizomes of the wheat grass and the consequent vigorous absorption prevents the moisture from penetrating deeply. The deeply rooted yellowbrush, quite unfitted to compete with the grasses in the surface soil, succumbs as a result. This illustrates the course of a plant succession which is of much economic importance. Wheat grass produces a large amount of forage and is especially well suited to the grazing of cattle and horses. Close grazing tends to destroy the wheat-grass cover and permits the growth of the needle grass and yellowbrush as well as a considerable variety of palatable weeds that are associated with these and are especially valuable for grazing by sheep and goats. Thus, the range, once the history of its vegetation is understood, can be held, by judicious management, in the most desirable stage of its development.[436]

Bisects through the dense mass of vegetation in a swamp show, for example, that cattails (*Typha*), arrowheads (*Sagittaria*), and smartweeds (*Polygonum*) secure light at different levels and that their rhizomes and roots occupy different levels in the soil.[470]

Three rather clearly defined root layers are evident in prairie. Some species absorb entirely from the surface foot or two of soil. Others extend their roots to depths of 3 to 5 feet, while some non-grassy herbs are branched but little in the surface foot or two but absorb water and solutes from depths between 2 and 15 feet. Clearly, a shallow-rooted grass and a very deeply rooted wild rose are carrying on their activities rather independently and with very little competition although they may grow on the same square foot of soil. The principle applies quite as well to cultivated crops as to natural vegetation.

The Migration Circle.—The movement or migration of plants by rhizomes, runners, seeds, etc., away from the parent individual or group may be accurately traced by means of the migration circle. Since migration usually takes place in all directions, a circle is more adapted to

the record than a quadrat. Where it is desired to trace such movements from the edge of a community, such as the advance of forest or shrubs into grassland, only an arc of the circle or series of concentric arcs need be used. The size of the circle is determined by the nature of the vegetation, especially its height, which directly affects the distance to which seeds or fruits are carried. The usual quadrat tape may be used for a circle with a radius of a meter. One end of the tape is fixed at the center of migration, and by describing arcs or circles the position of each species is determined. This is then indicated on the chart circle on the scale of 1:10. It is convenient to rule the chart so that the quarters are divided by several radii in order to aid in recording the individuals accurately and quickly. The distribution of many wind-borne seeds and fruits can best be studied during periods of high wind or under conditions of varying velocities, which should be measured. Sometimes this may be done to the best advantage when the ground is bared by burning or plowing or when the lower vegetation is covered with snow.

Using a Migration Circle.—Secure a number of fairly large and, hence, easily seen seeds adapted for wind distribution, such as elm, maple, birch, yellow pine, catalpa, etc. Place a tall stepladder in a recently plowed or snow-covered field. Mark off semicircles 5 feet apart in the direction in which the wind is blowing. Release a known number of seeds (*e.g.* 25) of each species, one at a time, from the top of the ladder and with the help of observers determine the distance the seeds are carried in falling to the earth. For each species, calculate the percentage that is carried 5, 10, etc., feet. The velocity of the wind should also be recorded (see p. 269). Do the seeds remain where they have fallen or continue their migration? Continue the experiment by observations on the distance to which fruits and seeds, other than those that are wind borne, are naturally distributed about the parent herb, shrub, or tree.

This method of study, somewhat modified, has shown that in burned or cut areas in the Douglas-fir region of the Pacific Northwest, the distance to which seed trees are capable of restocking the ground is limited to 150 to 300 feet. This led to an examination of the source of seed supply which gave rise to the young growth on extensive burns and it was found to be due to seed stored in the forest floor. These retain their viability, varying with the species, from 2 to 8 years or more.[241,242] The practical value of such results is far reaching. Similar studies have been made on the invasion of trees into natural mountain parks, *i.e.* local grassland areas surrounded by forest.

In reseeding depleted ranges, areas 15 or 20 rods long and 1 or 2 rods wide are sometimes enclosed. These plots, which are usually located in an open wind-swept area, are heavily seeded and the seed carefully worked into the soil. Soon the luxuriant vegetation produces an abundance of seeds, which find lodgment on the adjoining depleted areas, and in two or three seasons young plants are seen radiating from

these central colonies. The migration circle is applicable to a study of weed distribution and many other problems.[437]

Camera Sets or Tristats.—In temperate climates, the study of vegetation must be largely made during the growing season and time is often the limiting factor. The tristat method consists of repeatedly photographing the same area of vegetation. Three stakes are driven into the ground and one leg of the tripod placed on the top of each. The picture is taken in exactly the same direction each time with the camera at the same height. It gives a record of the development of the vegetation throughout the season and from year to year. Such photographs are not only quickly made but also bring out characteristics and illustrate features that do not lend themselves readily to description or measurement. The improvement of depleted range lands, for example, is marked by the appearance and spread of certain palatable species. Conversely, the deterioration caused by overgrazing is marked by their disappearance and a simultaneous increase in weeds. These changes may take place so gradually that even the trained investigator must have permanent records for comparison. They are best followed by permanent quadrats, but photographs showing the density and character of the vegetation are highly valuable.[114] By obtaining such a series of photographs from plots representing the area as a whole and by comparing them, a panorama of the change may be brought before the eye.[511]

The method is readily applicable in tracing the spread or decrease of poisonous plants, weeds introduced from centers of infection, shrubs introduced into grassland, rate of deterioration of fields of alfalfa, clover, or other crops, revegetation of denuded or bare areas, and, indeed, most of the phenomena concerned with a dynamic study of plants.

Ring Counts.—The age of a tree, shrub, woody vine, or half shrub and sometimes that of an herb may be determined by counting the annual rings of the aerial or subterranean stems. In many plants, such as pines and spruce, the annual growth is marked not only by the bud scars but also by the whorls of branches. Much valuable data may be obtained in regard to the general climate as indicated by rate of growth as well as in regard to the local environment under which the plant lives. The method of ring counts is important in determining the successive stages of developing vegetation and especially the sequence of dominants and subdominants. Trees usually invade grassland under cover of xeric (dry-habitat) shrubs, and other species, including shrubs, follow the trees because of their ameliorating effect on climatic conditions. Where trees overshadow shrubs on forest borders and doubt arises as to the sequence of invasion, ring counts usually reveal that the more xeric shrubs were the pioneers (Fig. 20).

It is sometimes of great importance to know the age of newly built islands, sand bars, or flood plains. Ring counts afford a reliable method.

In 1919, 100 years after a treaty with Spain had fixed the south bank of the Red River as the boundary line between what are now the states of Oklahoma and Texas, oil was discovered underlying certain lands which had apparently been added to the south bank by deposit but possibly

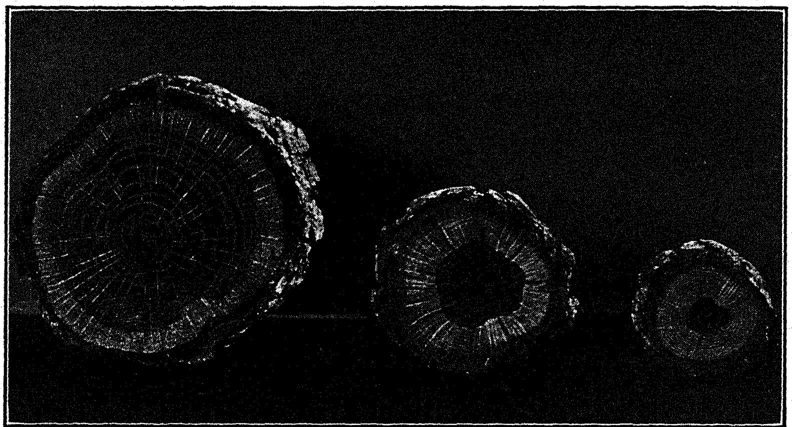

FIG. 20.—Cross-sections of three 20-year-old bur oaks from typical oak forests along the Missouri River. The largest, 4.5 inches in diameter, is from southeastern Nebraska where the precipitation is 32 inches; the smallest, 2 inches, from northeastern Nebraska, precipitation 23 inches; and the second from an intermediate station. The trees were 40, 25, and 18 feet high, respectively.

by a change in the course of the river's channel. A dispute between the two states followed, involving millions of dollars. Each claimed the oil lands. It thus became necessary to establish with certainty just where the south bank of the river was located 100 years earlier. By counting

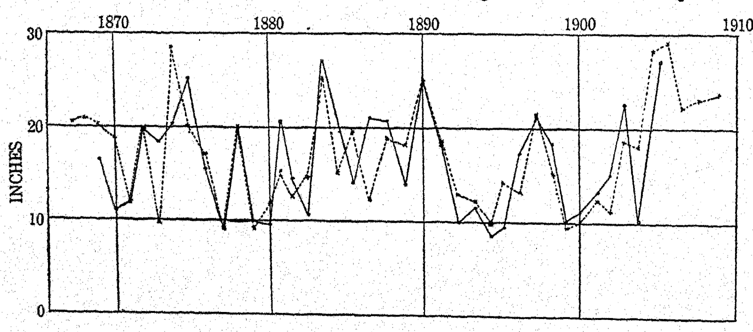

FIG. 21.—Actual rainfall (broken line) compared with rainfall calculated from growth of trees in Arizona. (*After Douglass.*)

the rings of numerous and well-scattered elms and other trees in the valley, as well as by a study of the rate at which the vegetation on the flood plain develops to a stabilized or climax condition, it was found that the oil lands had been on the Texas side of the river for more than 100 years.[457]

The close relation between actual rainfall and that calculated by means of the yearly growth rate of trees is shown in Fig. 21. Marked resemblances are found in certain individual rings over a wide range of the country in which climate is the only common factor. Thus, exceptional smallness in one ring (formed in 1851) has been found in trees over an area 750 miles wide, being shown by sequoias in California, yellow pines in New Mexico, and Douglas fir in Colorado. By a study of cross-identification of ring groups bounded by growth rings formed during years of marked peculiarity, it has been possible to tell the date when trees were felled.[144]

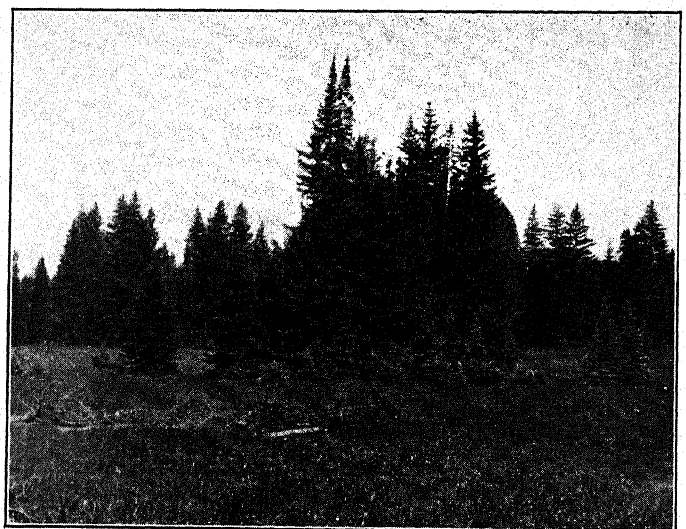

FIG. 22.—Reproduction cycle of Engelmann spruce (*Picea engelmanni*), in Colorado.

During 1918, an enormous seed crop of yellow pine on the Colorado plateau was followed by a year of precipitation unusually favorable to the growth of the seedlings. This coincidence had not occurred before for a period of 25 years. It will result in the repopulation of the area by an even-aged forest.[384] Ring counts in even-aged Douglas-fir forests of Oregon and Washington give us the date of previous burns and that of the new growth resulting. From ring counts on sagebrush and other desert shrubs, it seems clear that reseeding takes place only periodically and during especially favorable years[358] (Fig. 22).

In measuring width of annual rings, several precautions need to be taken. Trees growing in well-lighted, constantly moist habitats show a complacent growth, with rings all or nearly all the same size. Those growing with a limited water supply are more sensitive to rainfall and the ring width varies widely. A suppressed tree may, moreover,

have smaller rings in a favorable season than a dominant one in a poor season.[145] Where poor aeration and not water is the limiting factor to growth, as in beech trees in central Germany, the annual rings are widest during dry years (Fig. 23). Occasionally, a double ring is formed, when, for some reason (*e.g.* frost, caterpillars eating the leaves, etc.), growth is interrupted and again resumed during the same year.[14] Double rings frequently occur in certain warm climates, as in Arizona, with two seasons of rainfall. Further, it must be recalled that the growth-rate of trees decreases with age. The yellow pines of the dry Colorado plateau of

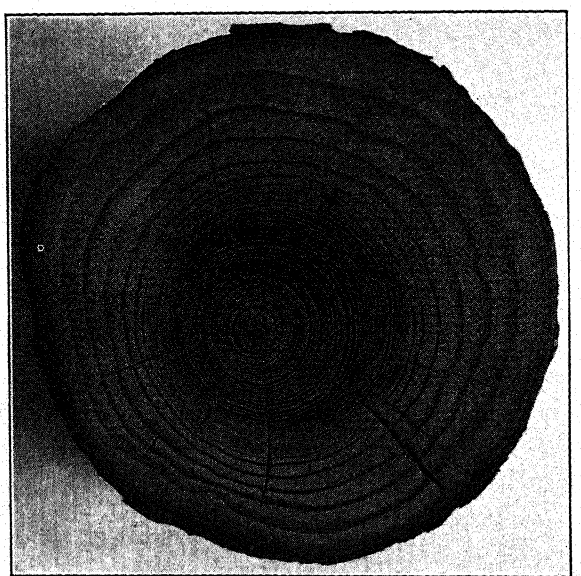

FIG. 23.—Section of a tamarack tree from a Minnesota swamp. Because of poor aeration in the wet peat it had reached a height of only 10 feet in 49 years. The swamp was drained in 1918, indicated by x, after which the tree grew 10 feet higher in the 7 years before it was cut down. (*After Zon.*)

northern Arizona have been shown, when corrections have been made for these factors, to represent the rainfall with an accuracy of 85 per cent.[146]

In practice, stumps resulting from lumbering or clearing are usually available in woodland, but often the trees must be felled as needed. The increment borer, which removes a small core of wood from circumference to center without injuring the tree, obviates this difficulty (Fig. 24). Since trees often grow more rapidly on one side than on the other, if better lighted or watered, borings should be made in two radii. The holes should be closed with wooden pegs driven firmly into the tree, to prevent infection by fungi, etc.

Determining the Age of Woody Plants.—Examine the stumps in a cut-over area. Are the trees of even age, that is, did most of them start at nearly the same time after

a previous cutting or fire? Making allowance for the growth of the seedling to the height of the stump, in what year did the group (or a particular tree) germinate or start from sprouts? Is the width of the annual ring about the same for the different trees of the same species? Compare the rate of growth of those on a hilltop and in a ravine. Are there any rings that are especially narrow or wide? What was the date of this dry or wet year? Does any tree show narrow rings abruptly followed by wider ones such as would occur if it were suddenly better illuminated as a result of the falling of an older tree? Examine a mixture (*mictium*) of young trees and tall shrubs, and determine if possible which were in possession of the area first.

In standing timber, employ an increment borer to determine the age and width of rings of a densely shaded (suppressed) tree and a well-lighted one of the same species or of one growing in a dry habitat and another equally lighted growing in a moist one.

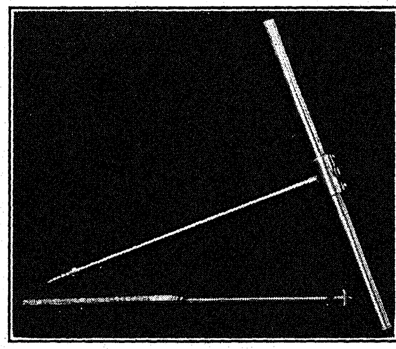

FIG. 24.—Increment borer and core 4 inches long from 27-year-old oak.

The Burn Scar.—Much information about the life history of a forest may often be obtained by a study of scars caused by fire. Not only the time of the fire but also its severity, the direction from which it came, and the extent of the burned area may be ascertained. *Surface fires,* which usually consume only the grasses and other herbaceous vegetation, may result in *ground fires* that burn more slowly down into the litter and mold, often following tree roots underground. They are much hotter and usually kill all trees and other vegetation.[546] Often they are limited to a few acres in extent.[472, 473] *Crown fires* race through the tops of trees at a high rate of speed, killing practically all vegetation in their path and leaving the soil in a sterile condition.[395]

Fires leave their traces on the woody plants perhaps as bark scars, more often as wood scars, and, especially on the edges of burns where the fire has died down, as heal scars, *i.e.* wood scars that have healed over. The time of a fire may be determined by counting the number of rings of wood put down since the burn scar was formed. Sometimes the burn scar may be double or even triple and thus give the dates of successive fires (Fig. 25). The direction from which the fire came is revealed by the side of the trees which was burned, and the extent of the area burned is coincident with the trees bearing scars, unless the fire became more destructive and killed all of the plants. In such areas, it is necessary to determine the age of the oldest trees, shrubs, and herbs, both standing and fallen, which have come in since the fire. If the growing season was not over when the fire occurred, root sprouts will show one more annual ring than trees and perennial herbs starting from seed which germinated the following spring. In order to secure the first annual

ring of trees, it is necessary to cut the seedling or sapling at the ground line or even below the ground line on steep slopes.[88]

Burns have a pronounced effect upon the composition and development of a forest. In the coniferous forests of the West, especially at high altitudes, they are almost invariably populated with lodgepole pine (*Pinus contorta murrayana*), a forest weed-tree which grows very rapidly, reproducing by seed at the age of 6 to 12 years and dominating the area until other pines, firs, or spruces grow up and shade it out. Repeated burns may result in an area being rather continuously occupied by lodgepole pine, a very inferior commercial type of forest. This is the case in much of the Rocky Mountain Park region, where at least 13 burns have been determined as occurring between 1707 and 1905.[88] The

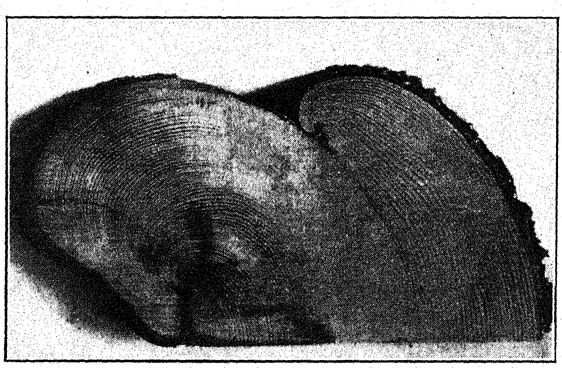

FIG. 25.—Section of the heal edge of a double-burn scar, furnishing the dates of two successive fires, Long's Peak, Colorado.

cambium of trees with thin bark like the white cedar (*Thuja plicata*) is much more easily killed by heat than a tree with thick bark like tamarack (*Larix occidentalis*). Differences in fire-resisting qualities of various shrubs also occur. Hence, a fire may greatly change the composition of a forest both by direct destruction of part of the plants and by altering the environmental conditions, especially light, for invaders. The original structure may often be determined by a study of adjacent, similarly located, unburned areas. That the history of the past aids in the present methods of forest management and their relation to future development needs scarcely be indicated.

Experimental Vegetation.—In the study of vegetation, many problems arise as to the causes of the particular plant distribution and the resulting structure. Measurement and comparison of the factors of the habitat usually throw much light upon the probable causes, but the answer can be made positively and decisively only by trying it out with the plants in question.[39,100] Much has been written, for example, about the causes for the treelessness of the prairies, but the question remained unanswered

until seedling trees were grown and their fate studied. It has been shown by experiments extending throughout many years, that in eastern Nebraska, because of drought, trees can not grow on the upland in competition with the grasses, even when planted in favorable small seed-beds. They are likewise unable to grow in low prairie because of the dense shade of the tall grasses. Fire, too, has been shown to be fatal to tree seedlings but much less harmful to grasses.[99]

The reason upland prairie species can not grow in tall marsh-grass (*Spartina*) swamps has been shown by transplanting large blocks of sod. Species that are not killed by deficient aeration, as shown by yellowing of leaves and rotting of stems, soon die as a result of shading. Ability to grow in alkali or acid soils may be tested in a similar manner. Forests offer excellent opportunity for determining the behavior of plants under different degrees of shading. Experimental areas in a desert valley, in an oak grove on the mid-slope of an adjacent mountain, and in the coniferous forest at its crest were each furnished with seeds or transplants of species from each of the three habitats. The experiment has yielded much direct information on the dissemination of species and barriers to ecesis.[328] Rodents, grasshoppers, and other animals often effectively prevent the successful invasion of plants from one community into another, although the fitness of the species for its native habitat may possibly be less than for the new one.

In such experiments, not only may the causes of failure or success be closely followed and the relative advantages of rootstocks or other storage and propagative organs determined, but also changes throwing light upon evolutionary sequence may be brought out. For example, species of sage (*Artemisia ludoviciana*), with leaves only slightly pubescent above, were reciprocally transplanted at various altitudes from the base of Pike's Peak to timber line with one (*A. gnaphalodes*) having foliage densely white-tomentose on both sides. After 3 years, it was found that plants of *A. ludoviciana* had greatly increased the hairiness of the upper surface and resembled *A. gnaphalodes*, while the latter had undergone little change. The value lies not only in the demonstrated change of one form into another but especially in the fact that the tomentum is shown to be more easily acquired than lost, *i.e. A. ludoviciana* is the primitive form and *A. gnaphalodes* the derived one.[96]

Extensive tests in seeding depleted ranges with native forage plants have been conducted in various portions of the country, many introduced species being used. Although the tests in the Southwest were largely unsuccessful, ranges in less arid climates have been greatly improved. As a result of over 600 reseeding experiments, directed by one forest ecologist using various cultivated grasses and other herbaceous forage plants, excellent results have been obtained.[381, 431] Not only the best species for sowing (timothy, Hungarian brome grass, rye grasses,

Kentucky bluegrass, and redtop) were ascertained, but also the best season for sowing, the best method of scattering and planting the seed, and the causes of failure were fully determined.[437]

Growing ordinary crops in a new country or new crops in a region long under cultivation is really a type of experimental vegetation. Much has been done to improve agriculture along such lines, as, for example, the introduction of winter wheat and alfalfa from the dry portions of Eurasia and of the sorghums from Africa into the drier portions of the United States. But only a beginning has been made when compared with the possibilities.

FIG. 26.—Relative growth of a native sunflower (*Helianthus rigidus*) in competition with prairie grasses (right) and in a quadrat where these competitors had been removed.

Importance of Field Experiments.—The importance of field experiments can not be overestimated. Often a simple experiment requiring little or no special apparatus throws much light upon problems of vegetation.[262] If, however, the problem demands, there should be no hesitancy in securing the needed apparatus and transporting it into the field. The experimental method simply means the observation of processes under controlled conditions. The nature and extent of the control will vary widely according to the end to be accomplished (Fig. 26). The fencing of an area against rodents, the cutting of a ditch to divert the water supply ordinarily received after heavy rains by one area to another, the supply of extra water to vegetation in times of drought, or the addition of fertilizers are examples of field experiments which have given valuable results.[159]

Why regeneration of beech woods in England and Scotland is so poor was determined by fencing small areas. From some areas, rabbits were excluded; from others, both rabbits and birds; and from still others, field mice as well. By placing beechnuts in each enclosure both on the surface and within the forest litter, it was found that rabbits ordinarily ate very few seeds, birds secured only those on the surface, but mice destroyed almost the entire supply, except a few overlooked in the duff. This simple experiment established the fact that, in a large measure, mice are responsible for the failure of the rejuvenation of beech forests.[556]

An exact knowledge of the amount of damage done to the range by rodents and especially of the rate and degree of recovery of the various

types of vegetation after rodents have been eradicated has been obtained in a similar manner. Exclosures were made against rodents and cattle, against cattle alone, and against cattle where rodents had been killed. Clipped quadrats from these as well as from enclosures inhabited by jack rabbits and others inhabited by kangaroo rats showed the heavy toll of vegetation taken by these pests, a matter of grave importance, especially in times of drought[523] (Fig. 27).

Experiments need by no means be confined to native vegetation. Many ecological processes may be conveniently studied in a garden, orchard, or grove, and it should be kept clearly in mind that what man calls agriculture is, in a large measure, the making of an environment

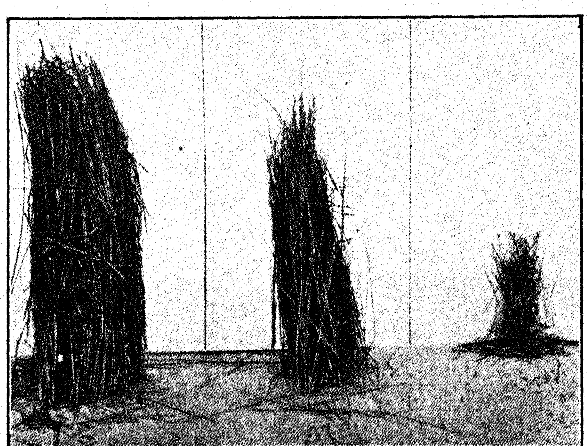

FIG. 27.—Wheat grass from clipped quadrats; (left) where both cattle and prairie dogs have been excluded, (center) where cattle only have been excluded, and (right) on the open range. Grand Canyon, Arizona. (*After Taylor and Loftfield.*)

more or less suitable for crop plants. Fundamentally, the growth and functioning of the plant depend upon the nature of the environment and the adjustment to it and not directly upon cultural practices. The latter only modify the relation of the plant to the environmental complex.

Mapping.—Just how to begin the study of vegetation may usually be decided by the object in view. In general, a preliminary survey or reconnaissance precedes intensive work in any particular area. This is true whether all the communities in the region or only certain ones are to be studied. Such a survey gives a general knowledge not only of the various types of vegetation but also of the conditions under which they occur and enables the investigator to choose typical areas for more detailed study.

The mapping of a suitable area furnishes excellent experience with extensive vegetation, especially if a considerable number of communities are encountered, for the relations of these have to be closely studied in

order to present them on a map. A general idea of the broad features of vegetation will have to be formed. This focuses the attention upon particular problems and compels one to make a decision about the vegetation studied. It must first be determined what plant communities are to be mapped, their extent, transition into other communities, etc. In this way, the larger communities should be distinguished, recorded, and characterized, and their relation to topography, exposure, and soil type determined in a general way. Typical examples of each community must be rather thoroughly examined, their more important species listed, and the main features of their structure determined. In such work, it must be clearly kept in mind that the aim is to get a general idea of the whole area. Detailed work in any community will follow as a natural sequence.

Aside from the map, complete field notes should be taken and a very valuable supplement to these are photographs not taken at random but to illustrate typical vegetation. These greatly help when it comes to writing up the field notes in connected sequence. The amount of detailed information obtained and the accuracy of the mapping will vary, of course, with the size of the area under study.[519]

Community Charts.—Much may be learned about the structure and development of individual communities by making a large-scale chart of a relatively limited area. Such charts represent the details of the vegetation of a small area on a large scale. They are made by dividing the area for study by means of cross-tapes into units usually a meter square.

The boundaries of small, well-defined, uniform communities can be plotted to within 3 inches of their actual position and the position of large, isolated, individual plants or clumps of vegetation definitely located. Much of the detail of the actual structure of the vegetation may be shown by means of appropriate symbols. These should be so simple that the map may be readily interpreted. Cross-hatching or distinctive shading may be used and transitional areas shown by the overlapping of the two kinds. It is well to trace the original chart in ink and to keep it for reference, since the chart method reaches its greatest usefulness only when the area is permanently marked and changes occurring from year to year recorded (Fig. 28).

Many situations warrant permanent mapping, but it must be understood that the chart in itself is of little value unless it is a characteristic sample of the detailed structure of a widely distributed community. It should show some definite distribution of vegetation in relation to habitat or be of use in solving some problem in the development of vegetation, etc. For example, the distribution of communities or zones about marshes or lakes may be correlated with water content, or those in alkaline areas with salt.

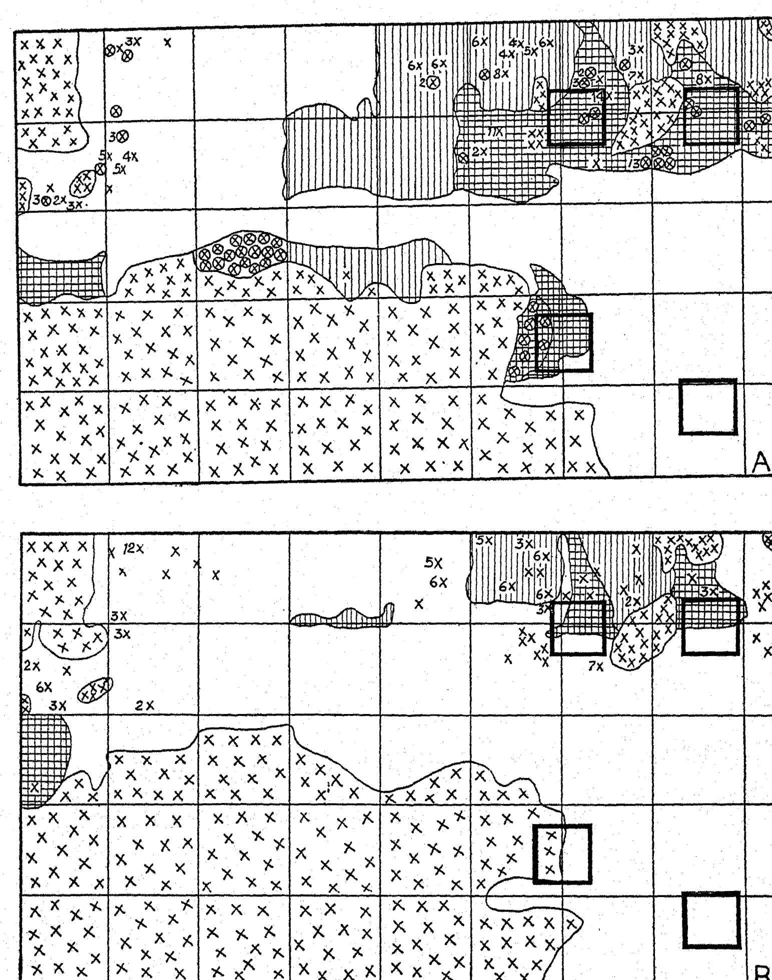

Fig. 28.—*A*, an area 41 by 25 feet in an overgrazed pasture at Lincoln, Nebraska. It was marked off in 5-foot squares and mapped in June, 1924, one month after excluding the cattle. *x*, shrubs, mostly wolfberry (*Symphoricarpos*). *x* with circle indicates those starting in 1924. The number of individual stems is indicated only outside the areas dominated by shrubs; vertical hatch, bluegrass (*Poa pratensis*); cross-hatch, buffalo grass (*Bulbilis dactyloides*); unmarked areas, wheat grass (*Agropyron smithii*). The positions of four quadrats are indicated by squares.

B, same area at the end of the third growing season, August, 1926.

Has bluegrass increased or decreased its territory? Has buffalo grass extended its area anywhere? What is replacing it in a large measure? Note that the shrubs have extended their front only slightly and not uniformly. By counting the squares, or more accurately by placing a heavy cardboard under the map and using a planimeter, ascertain the percentage decrease of bluegrass and buffalo grass and the increase of wheat grass. All three grasses formed dense sod in which only a few other species occurred.

In the study of succession, community charts are often indispensable. By their use, the changes from year to year, such as the shifting of ecotones following invasion of one community and the disappearance of another, may be traced in detail. By this means, changes are permanently recorded, the time element determined, the causes of change often automatically revealed, and a record obtained the accuracy of which can not be impugned. This greatly supplements the study of change by inference, *i.e.* piecing together the course of development from the various kinds of communities found in the region.

CHAPTER III

THE UNITS OF VEGETATION

The climate over an extended area of land, such as a continent, is usually very diverse and conditions for plant growth correspondingly different. Distance from the ocean, differences in latitude and altitude, etc., all profoundly affect precipitation and temperature as well as other climatic factors. Vegetation responds by its distribution into groups, each of which is in close equilibrium with its particular climatic complex. Such major groups as forest, grassland, and desert have long been recognized.

The Formation.—The plant formation is the major unit of vegetation. It is a fully developed or climax community of a natural area in which the essential climatic relations are similar or identical. Each formation is a complex and definite organic entity with a characteristic development and structure. It is a product of the climate and is controlled by it.[90] The deciduous forest of the East, the coniferous forest of the Great Lakes region, the tundra of the far North, and the grassland of the central West are examples. Every formation is delimited by climate. The rainfall and evaporation of the Ohio Valley region are very different from that of the prairie-plains. The temperature of forest-covered mountain slopes is quite unlike that of the alpine meadow above timber line. A climate marked by a moderately long, warm, fairly humid summer, which is favorable to trees with deciduous leaves, and by winters during which the surface soil is frozen and absorption retarded will be characterized by a deciduous forest.

While the greater portion of a climatic region is occupied by the climax vegetation characteristic of it, many areas in which new or denuded soils occur show various stages of development. In the deciduous forest climax, for example, marshes may be populated by cattails and dry ridges by shrubs. But these are only stages in the development of the vegetation. When the annually accumulating plant debris with its admixture of water- and wind-borne soil builds up the marshy lowland, trees will ultimately occupy the area, because the climate is congenial to trees. When the decaying roots, stems, and leaves of the shrubs, etc., add enough humus to cause the soil of the eroding ridge to hold more water, it, too, will become forested (Fig. 29). Just as a tree passes through the seedling and sapling stages and then grows to maturity, so, too, the formation arises, grows, matures, and dies. The formation,

moreover, like the plant, is able to reproduce itself, as may be seen after fire, lumbering, or other catastrophe to the vegetation. This developmental point of view is exceedingly important, since it furnishes a dynamic working basis for the classification of vegetation.[361,369,518]

The major divisions or units of the vegetation of a continent are the highest expression of vegetation possible under a particular climate, grasses, sedges, and lichens in tundra, scattered shrubs in sagebrush desert, and dense jungles of trees, shrubs, and lianas in the tropics. Consequently, the formation is designated as a climax or climax formation. The

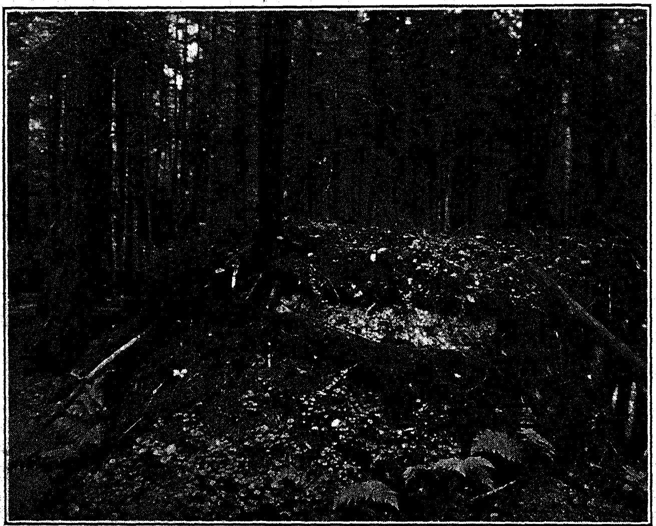

FIG. 29.—A boulder in a coniferous forest of New York on which the soil blanket has become heavy enough to support approximately climax forest vegetation. (*Photo by W. L. Bray.*)

character of the climax is revealed by the dominants or controlling species of which it consists. All these belong to the same vegetation-form, which represents the highest possible type under the prevailing climate. In grassland, the climax dominants are all grasses or sedges; in forest, they are trees; and in chaparral, shrubs. In every formation, one or more of the dominant species ranges widely and often throughout, *e.g.* white pine (*Pinus strobus*) in the Great Lakes climax and grama grass (*Bouteloua gracilis*) in the grassland formation. The majority of the dominant genera, moreover, extend throughout the formation, though represented by different species, *e.g.* various scrubby oaks, sumacs, cherry, etc., in chaparral. Hence, the formation is named after its most widely spread and important dominants. Examples are the cedar-hemlock (*Thuja-Tsuga*) or coast forest climax and spruce-larch (*Picea-Larix*) or boreal forest climax (Fig. 30). A complete list of the climaxes of North

America is given on page 425, and an idea of their relative expanse may be gained by an examination of the Frontispiece.

The difficulty of drawing exact boundaries between formations may be appreciated when it is realized that developmental studies have not yet determined whether or not all of the climatic areas are actually occupied by the type of vegetation which they may ultimately support. Part of the area covered by chaparral, for example, may have a forest climate, the trees being held in check by repeated fires. Desert scrub may really have a grassland climate in part, the grasses having largely disappeared as a result of severe overgrazing during times of drought. Large areas in Illinois, Iowa, and Missouri were once occupied by grassland, which

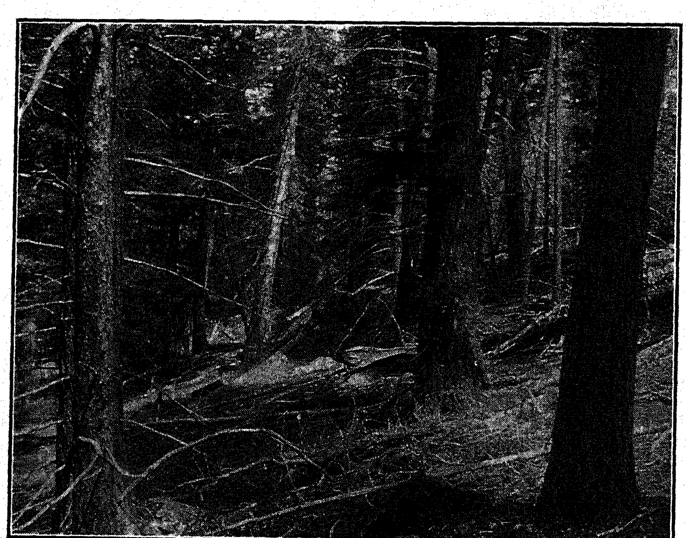

FIG. 30.—Climax forest of Douglas fir (*Pseudotsuga mucronata*) in Colorado.

still persists in a forest climate. The shrubs and trees were held in check in their competition with the grasses either by unfavorable soil conditions, such as poor drainage, or by fires, grazing, or mowing.

In delimiting climates and climaxes, the plant is the ultimate criterion, and climatic measurements must be interpreted in terms of plant growth. From the human standpoint, eastern Washington and central Kansas possess distinct climates, but in terms of wheat production and grassland vegetation, they are very similar. Likewise, the winter in Saskatchewan is long and the summer short, while in Texas just the reverse is true. But the short growth-period of grama grass fits into the short summer of Saskatchewan as readily as it does into the moist, early summer of Texas, with the result that this dominant covers large areas in both.

The Association.—Every climax formation consists of two or more major subdivisions known as associations. These are climax communi-

ties associated regionally to constitute the formation. For example, the portion of the grassland formation between the deciduous forest climax and the Rocky Mountains consists of true prairie in the best watered eastern part, mixed prairie in the area of intermediate rainfall, short-grass plains in the drier western portion, and desert plains in the very arid southwest. Each of these constitutes an association. Likewise, the oak-chestnut forest, the oak-hickory forest, and the maple-beech forest are the associations of the deciduous forest formation (Fig. 31).

An association is similar throughout its extent in physiognomy or outward appearance, in its ecological structure, and in general floristic composition. To illustrate: The mixed-prairie association is similar

FIG. 31.—Detail of the oak-hickory association. A society of May apple (*Podophyllum*) occurs on the forest floor.

everywhere in having an upper story or layer of tall-grass dominants and a lower one of short, mat-forming grasses. Needle grass, wheat grass, or June grass overtop the buffalo grass and grama grass or sedges of similar, low-growing habit. These, like many subdominant legumes, composites, etc., range throughout the association.

The Associes.—The associes is the developmental equivalent of the association. This name is used where the community is not permanent but is replaced by another in the process of development or succession. A community of cattails, bulrushes, and reeds in a swamp represents only a temporary stage of development, *i.e.* an associes. As the pond shallows, they will be replaced by other kinds of plants. Similarly, the invasion of shade-enduring red oaks or lindens into a light-demanding bur oak-bitternut-hickory forest clearly indicates that the bur oak and hickory will sooner or later be shaded out. Hence, the bur oak-bitternut

hickory forms an associes (Fig. 32). Associes of shrubs, such as hazelnut (*Corylus*), coralberry (*Symphoricarpos*), etc., occur after lumbering in a deciduous forest, just as those of birch (*Betula*) and aspen (*Populus*) develop in northern coniferous forest after fires.

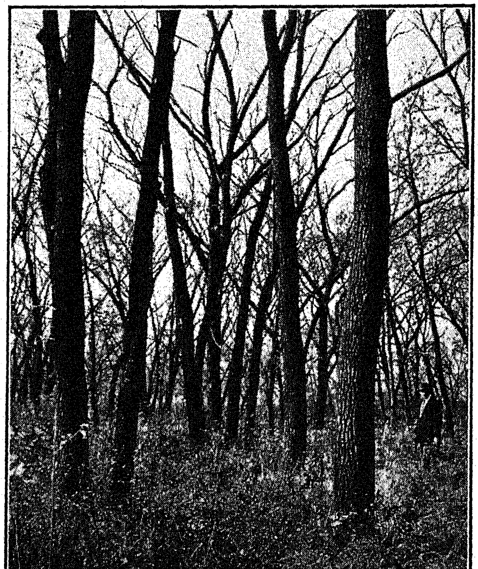

FIG. 32.—An associes of walnut (*Juglans*) and elm (*Ulmus*) on a flood plain.

The Consociation.—Every association consists of several dominants, sometimes ten or more, each of which constitutes a consociation. The true prairie (*Stipa-Sporobolus*) association comprises the following dominants: needle grasses (*Stipa spartea* and *S. comata*), dropseed (*Sporobolus asper*), June grass (*Kœleria cristata*), wheat grass (*Agropyron smithii*), and little bluestem (*Andropogon scoparius*). Any one of these may dominate an area more or less exclusively or at least to such an extent that it is more important than any of the others. Thus, within the true prairie association there occur wheat grass, needle grass, etc., consociations. Since the dominants approach each other in habitat requirements, they are frequently mixed in various degrees. In the oak-hickory association, for example, while the dominants may be more or less equally intermingled, each frequently occupies extensive areas in rather pure stands (Fig. 33). In the Rocky Mountains, forests of nearly pure yellow pine (*Pinus ponderosa*) occur over vast areas; others support extensive forests of Douglas fir (*Pseudotsuga*). These represent two consociations of the montane forest formation.

The separation of the dominants into consociations may be due to minor variations in the habitat occupied by the association, some

parts of which may be slightly more suitable for one dominant and some for another, while other areas are intermediate so that mingling of dominants occurs. It sometimes happens that one dominant occupies an area so completely as to exclude the others simply because it invaded first, although the habitat was equally suitable for all.

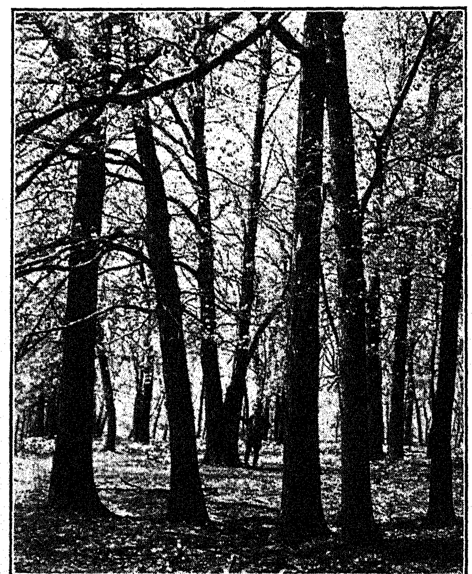

FIG. 33.—Consociation of red oak (*Quercus rubra*).

The Consocies.—In an associes (developmental association) each dominant forms a consocies (developmental consociation). The reed swamp furnishes an excellent illustration. Here *Typha*, *Phragmites*, and *Scirpus* may be intermixed, but more usually each occurs as a consocies in definite areas, the bulrush usually in the deepest water and the reed in the shallowest. Consocies of hazelnut, aspen, and birch are regularly replaced by forests when the latter again develop after lumbering or fire (Fig. 34). Sand-binding grasses on dunes which are being forested furnish examples of associes with their consocies, as does also the shrub stage which usually precedes the trees. Indeed, once the development of vegetation is understood, many dominants will be found to be relatively transient.

The Society.—Within the area of vegetation under the control of a dominant, *i.e.* within the consociation, certain subdominant species may exert local control. The many-flowered psoralea (*Psoralea floribunda*) is often so abundant in the needle-grass (*Stipa*) consociation that for a time it quite obscures the grasses. The same is true of the daisy fleabane (*Erigeron ramosus*), indigo plant (*Amorpha canescens*), and

numerous other herbs (Fig. 8). These local communities are called societies. A society is a community characterized by one or more subdominants.

The dominants strongly influence and sometimes largely determine the rest of the species belonging to the association, especially by shading. A subdominant is a species which is dominant over portions of an area already marked by the dominance of consociation and association. That is, the society is a localized or recurrent dominance within a general dominance. In grassland, societies are usually conspicuous for only a part of the season. While the dominants such as needle grass, wheat grass, or buffalo grass are present and controlling at all times, *Psoralea,*

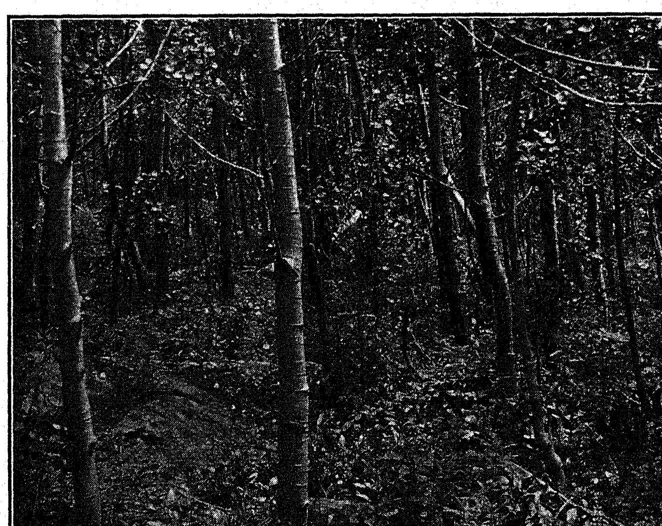

FIG. 34.—Consocies of aspen (*Populus tremuloides*).

Erigeron, and *Amorpha* are conspicuous and play an important rôle in vegetation only at certain times of the year. They are subdominant or subordinate to the grasses as is shown by the fact that under adverse conditions, such as decreased rainfall, they are among the first to disappear.

Societies in forests are found only beneath the primary layer of trees, and their subdominance is obvious. Such societies as gooseberries, witch-hazel, Jack-in-the-pulpit, and strawberries are illustrative. In woodland, societies consist of herbs and shrubs; in grassland, of non-grassy herbs and undershrubs. Societies may not be confined to a particular consociation but may occur widely throughout the association. They may occur more or less uniformly over wide stretches or be repeated wherever development or physical factors warrant.

Two kinds of societies may be differentiated. The most casual observation shows that in a climate with well-marked seasons, different species of an association make their most vigorous growth, flower, and fruit at different periods of the growing season. A little study shows that the species tend to fall into rather distinct groups, the activities of each group giving a distinct *aspect* to the association. Thus, in the true prairie of eastern Nebraska, certain sedges (*Carex*), prairie cat's-foot (*Antennaria*), and prairie windflower (*Anemone*) stand out conspicuously during April against the brown background of dry grasses and herbs. They constitute the early spring or *prevernal aspect*. Each species forms an aspect society. During May, the purple and blue of societies of ground plum (*Astragalus*), the massive cream-colored racemes of false indigo (*Baptisia*), and the bright yellow heads of *Senecio*, with many other spring or *vernal* societies, add tone to the landscape. But by June most of these have waned and the prairies until late July are characterized by extensive summer or *estival* societies of many-flowered psoralea (*Psoralea*), daisies (*Erigeron*), niggerhead (*Brauneria*), lead plant (*Amorpha*), rose, and many others. Then, again, the scenes are shifted. The purple of the *autumnal* societies of blazing stars (*Liatris*) is mixed with the yellows of goldenrods (*Solidago*) and sunflowers (*Helianthus*). These with the asters and numerous other species mark the end of the growing season.[225]

Open chaparral and woodland in early spring present definite aspect societies of prevernal and vernal shrubs and herbs, these being especially pronounced since the late leafing of trees and shrubs admits more light.[299] The estival and autumnal aspects may be less conspicuous but each shows the vigorous development of certain subdominants, especially among the more favorably situated taller species. In boreal and alpine regions, the number of aspects is often but two, vernal and estival, and the societies correspond.

The great majority of associations, including all of those whose dominants are tall plants, exhibit layers below the general level of the dominants. These are especially conspicuous in open woodland but also occur in chaparral, in grassland, and elsewhere. Commonly four and often six or more layers may be distinguished.[480] They are not usually continuous but more or less interrupted, largely depending upon the amount of light passing through and between the crowns of the trees and, in part, upon soil moisture and other soil factors. In open oak forest, the layer of trees overtops the layer of shrubs beneath which occur the herbaceous layer and, very near the ground, the moss-lichen-fungus layer. While a dense spruce forest may have only one, the ground layer, a tropical rain forest has six or seven distinct strata. Various intermediate conditions occur. Sometimes a second tree layer occurs under that of the dominants, *e.g.* ironwood (*Ostrya*) in deciduous forest, and often a tall herbaceous layer overtops a shorter one.

Each layer of vegetation has an environment quite different from that of the others. The crowns of the trees are exposed to full sunlight and often to considerable wind, while all the other strata are more or less protected from both. Since light decreases as the soil level is approached, it is usual for the societies of the lower layers to appear first—*e.g. Anemone, Erythronium, Vagnera,* etc., early in the season, often simultaneously with the blossoming of the shrubs above, such as hazelnut, prickly ash (*Zanthoxylum*), etc., but usually before the shrubs and trees have come into full leaf (Fig. 35). Such communities are designated as *layer societies.*

Fig. 35.—Layer of dogtooth violet (*Erythronium*) in the early spring aspect of the oak-hickory forest at Lincoln.

The Socies.—Societies of developmental communities, such as lobelias or mints in a cattail consocies are termed socies. Phlox and waterleaf (*Hydrophyllum*) communities of a flood-plain forest associes are properly designated as socies, a term which at once denotes temporary rather than permanent subdominance. Many ruderals (weeds) form socies (Fig. 36).

The Family.—In bare or recently populated areas such as railway embankments, alluvial deposits, etc., the vegetation frequently consists of groups of individuals belonging to a single species. Such a community of ragweeds, sunflowers, stinging nettles, etc., where all the individuals belong to a single species, is a family (Fig. 37).

Other examples are the green slime (*Protococcus*) on the moist bark of a tree, the growth of a fungus, such as *Polyporus,* on a fallen log, a very clean field of corn, or a community of Jack-in-the-pulpit on the

otherwise bare area under a forest canopy. While the family often springs from a single parent plant, this is not necessarily the case. It

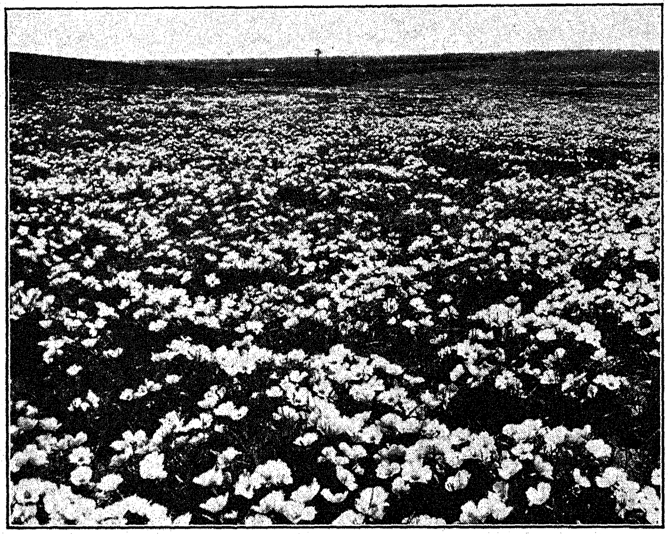

FIG. 36.—Socies of an evening primrose (*Anogra albicaulis*) in a fallow field.

FIG. 37.—A family of knotweed (*Polygonum majus*) on a talus slope.

may consist of only a few individuals or it may extend over a large area. The family, however, is usually a small unit and is especially typical of early stages of development, rarely being found in stabilized vegetation,

except where local disturbance has occurred, *e.g.* a family of wire grass (*Aristida*) on a gopher mound.

The Colony.—As the individuals of a family become more numerous, usually adjacent families merge, or migrules from one family may invade another at some distance. Sometimes two or more species may enter a bare area simultaneously. In either case, such an initial community is termed a colony. Colonies are practically always a consequence of invasion and, therefore, like families, are characteristic of early vegetational development. Colonies of lichens occur on rocks, colonies of weeds in neglected gardens or lowlands subjected to periodic overflow, colonies of sand binders on wind-formed dunes, and colonies of fireweed (*Chamaenerion*) and firegrass (*Agrostis hiemalis*) are frequent in burned woodland, etc. Usually, they are easily identified, since they occur in bare areas or open vegetation. When they occur in stabilized vegetation it is usually where a small bare area permits invasion. If two or more invaders populate the bare area, the community is a colony; if only one, it is a family. While a clean field of corn represents a family, a weedy one is a colony. Both family and colony are developmental and no corresponding climax units occur.

To Outline the Major and Minor Communities of a Region.—After a number of field trips in which examples of each unit of vegetation have been examined, make a summary list of the plant formations and associations visited, the associes studied, and typical consociations and consocies observed. What are some of the more important societies? Name some developmental societies or socies encountered. What species form families and colonies in the region and under what conditions?

The Study of Communities.—It must not be supposed that one can distinguish the units of vegetation of any given area offhand or by superficial examination with any greater degree of accuracy than one can distinguish the different structures within a plant without careful study. Until sufficient examination has been made by means of ecological methods to warrant placing any area of vegetation in a particular formation, association, or consociation or to designate certain parts as families, colonies, or societies, each should be called a community, a term which implies no definite rank. Moreover, all ecological investigators have not given the same rank to equivalent units of vegetation. This has resulted often from the limited area studied, *i.e.* its relations to adjacent major units were not determined, or sometimes from the fact that the studies were made in transitional areas.

There are seldom sharp lines of demarcation where one of the communities of higher rank merges into another. They usually overlap forming a mixed community. Such transitional areas are termed *ecotones*. In level country where conditions are fairly uniform, *e.g.* between true and mixed prairie, the ecotone may be broad and indefinite.

But on mountains or steep hillsides or in the associes about lakes or ponds, etc., communities may be very definitely delimited. By careful study, it is always possible to analyze the vegetation of a region into its natural communities. A study of the mass of vegetation making up the community, called *synecology*, necessarily focuses attention upon the individual species of which it is composed. It is one of the best ways of suggesting the most important problems presented by the component species, *i.e.* problems of *autecology* or the ecology of the individual.[102,247,357]

CHAPTER IV

PLANT SUCCESSION

As vegetation develops, the same area becomes successively occupied by different plant communities. This process is termed plant succession. Within a region, the same final or climax stage results from this series of successive stages whether they start in open water, on solid rock, or on denuded land. Successions beginning in ponds, lakes, marshes, or elsewhere in water are termed *hydrarch*, and the different stages of the series or sere constitute a *hydrosere*.[110] Although the movement from initial stage to climax is usually continuous, when one group of dominant plants reaches its maximum the change is clearly marked. This is especially true when one life-form, such as that of floating plants, gives way to another, such as reeds and rushes. The stages and the processes operative in bringing about plant succession in the various seres will now be examined.

A HYDROSERE

Submerged Stage.—Near the shores of a lake or, perhaps, throughout its extent, if the water is less than 20 feet in depth, may be found many species of plants growing entirely submerged. These are the pioneers of the hydrosere. Prominent among them are several species of flowering plants such as water weed (*Elodea*), pondweeds (*Potamogeton*), water milfoil (*Myriophyllum*), and naiads (*Najas*). These grow at various depths, rooted in the muddy or sandy bottom, depending somewhat upon the species but especially upon the clearness or turbidity of the water. They often form dense masses of vegetation. Submerged buttercups (*Ranunculus*), bladderworts (*Utricularia*), and eelgrass (*Vallisneria*), together with numerous algæ, varying in size from microscopic forms to the herb-like *Chara*, help to fill the water more or less completely with a tangled vegetation. The vegetation forms rather open patches in some places but a continuous, tangled, aquatic garden in others. Indeed, the density of growth of some of these submerged plants is sometimes so great, especially in late summer when they are fully grown, that boating may become difficult if not impossible.

The growth of this submerged vegetation year after year has a very marked effect upon the habitat. Material eroded by streams and transported into the lake is deposited about the plants because they form a direct obstacle to its advance, and especially because they slow down the currents. Moreover, when the plants die their remains sink to the

bottom where, because of insufficient oxidation, the vegetable debris and the dead animals associated with it are only partially decomposed, forming a mass of humus which cements the mucky soil together, making it firmer. The result of these reactions brought about by the submerged plants is to shallow the water by building up the bottom of the lake. Obviously, this process is disadvantageous to the present occupants and ultimately there is formed a suitable water depth and a rich substratum for invaders.

Floating Stage.—Where the water is only 6 to 8 feet deep, various species of floating plants begin to invade the area occupied by the pioneer,

FIG. 38.—Water lilies (*Nymphæa polysepala*) in a lagoon, illustrating the floating stage of a hydrosere.

submerged plants. They migrate mainly by rhizomes from their stronghold in the shallower water. Chief among them are various water lilies (*Nymphæa*, *Nelumbo*, *Castalia*), pondweeds (*Potamogeton*), and smartweeds (*Polygonum*), although many others may occur. Usually, several species are associated, sometimes only two, and often a single representative covers large areas (Fig. 38). All are rooted in the mud. Nearly all have rhizomes, sometimes several feet in length, or stems rooting at the nodes, while the petioles or stems, varying in length with the depth of the water, permit the broad leaves to float on the surface.

At first, the floating plants are intimately associated with the submerged species, particularly those that grow best in the shallowed water. But as the invaders increase in numbers, gradually spreading year by year, their leaves occupy more of the water surface and the light for submerged

plants is decreased. These must migrate into deeper water. Frequently, the masses of unattached floaters, such as duckweeds (*Lemnaceæ*), water hyacinth (*Eichhornia*), etc., cover the surface and aid materially in reducing the light. Because of the dense tangle of stems, much water-borne soil is deposited in the floating-plant zone, while the debris formed by the decay of these rather massive species rapidly builds up the substratum. Spring freshets may, wholly or in part, wash away this accumulated material, in which case the floating stage persists for a long time. But usually the soil-building process goes on so rapidly that within a few years at least the shoreward margin of the floating plant zone can be invaded by swamp plants. Water that is too shallow is distinctly unfavorable to floating species, and this community, even if uninvaded, would ultimately make the habitat so unfit for itself that floating plants would disappear.

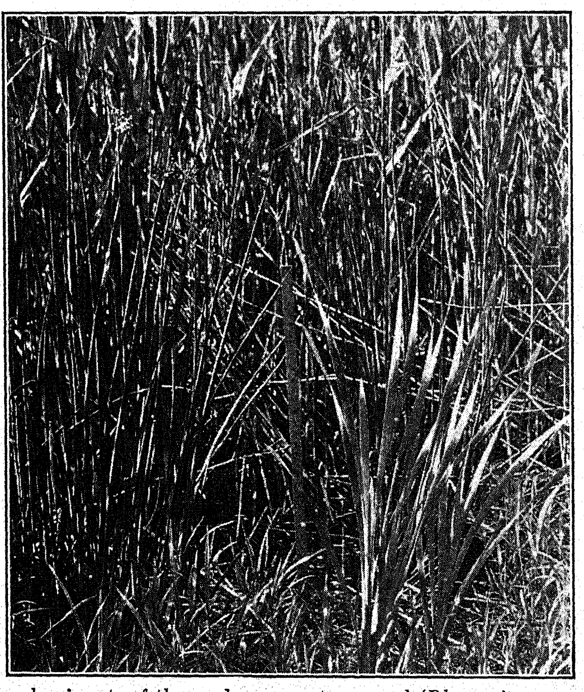

FIG. 39.—Three dominants of the reed-swamp stage, reed (*Phragmites communis*), bulrush (*Scirpus validus*) in blossom on left, and cattail (*Typha latifolia*).

Reed-swamp Stage.—With the continued shoaling of the water, invasion becomes possible for plants that root at the bottom and are partly submerged but whose foliage is raised above the surface of the water. The tall bulrush (*Scirpus validus*), cattail (*Typha*), and reed (*Phragmites*) may invade the territory occupied by the floating plants where the water is 1 to 4 feet deep. The bulrush usually grows in the

deepest water, sometimes in excess of 6 feet, and reeds in the shallowest, but they are often intermixed (Fig. 39). All have large, much-branched rhizomes, and where establishment of seedlings is unsuccessful, invasion is still possible. Associated with them or in similar habitats are other bulrushes, bur reeds (*Sparganium*), wild rice (*Zizania*), etc. Like the preceding plants, their tall stature and dense, sod-like growth exert a controlling influence. Obviously, the floating plants are at a great disadvantage as regards light. As the reed-swamp community develops, they largely or entirely disappear, moving outward into deeper water in the wake of the submerged species.

The reaction of the reed-swamp plants is not only to shade the surface of the water but also to build up the lake shores by retaining the sedimentary materials washed into the lake and by the very rapid accumulation of plant remains. Not only is the plant population much denser than before but also mechanical tissues, which resist decay, are much more highly developed in plants with aerial organs. Thus, the water depth is gradually decreased. Many secondary species such as arrowheads (*Sagittaria*), water plantain (*Alisma*), sweet flag (*Acorus*), smartweeds (*Polygonum*), etc., aid in bringing these reactions about and ultimately in making the habitat less fit for most species of the reed-swamp stage.

Sedge-meadow Stage.—The cattails, bulrushes, etc., develop less vigorously with a lowering of the water level, and other species invade their territory. Favored by an increasing amount of light, as the former occupants disappear, they gradually change the reed swamp into a sedge meadow. Numerous carices (*Carex*), rushes (*Juncus*), and spike rushes (*Eleocharis*) form, with their tough, tangled rhizomes and slender, copious roots, sod-like mats of vegetation (Fig. 40). The soil gradually becomes too dry for plants of the preceding community but is still very wet in spring and early summer when it may be covered with several inches of water. But later in the season, this surface water disappears and the soil may be merely saturated, the water level sinking a few inches below the surface. Varying degrees of wetness may be found depending upon the progress of development and irregularities of topography (Fig. 41). Islands of bur reeds or cattails may persist in depressions for a long time as relicts of the old community and indicators of a former swamp. Many herbaceous species occur intermixed with the patchwork of the *Eleocharis-Carex-Juncus* complex. Examples of these are mints (*Mentha, Teucrium*), marsh marigold (*Caltha*), blue flag (*Iris*), bedstraw (*Galium*), water hemlock (*Cicuta*), cotton grass (*Eriophorum*), and bellflower (*Campanula*). All react upon the habitat by binding water-carried and wind-borne soil, accumulating plant debris, and transpiring enormous quantities of water. The spike rush alone may add a few millimeters of humus each year. Finally, the marshy sedge meadow

becomes too dry for these water-loving plants (*hydrophytes*) to thrive. They are gradually replaced by species of another community. In dry

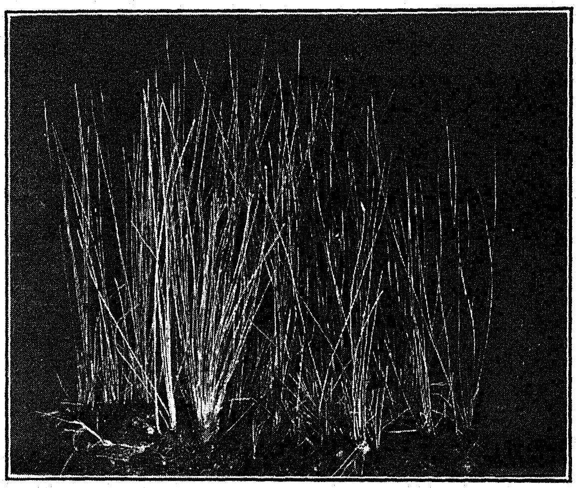

FIG. 40.—Spike rush (*Eleocharis palustris*) characteristic of the sedge-meadow stage of a hydrosere. The plants are about 18 inches tall.

climates, this may be grassland or some other xeric climax; but in more moist ones, woodland.

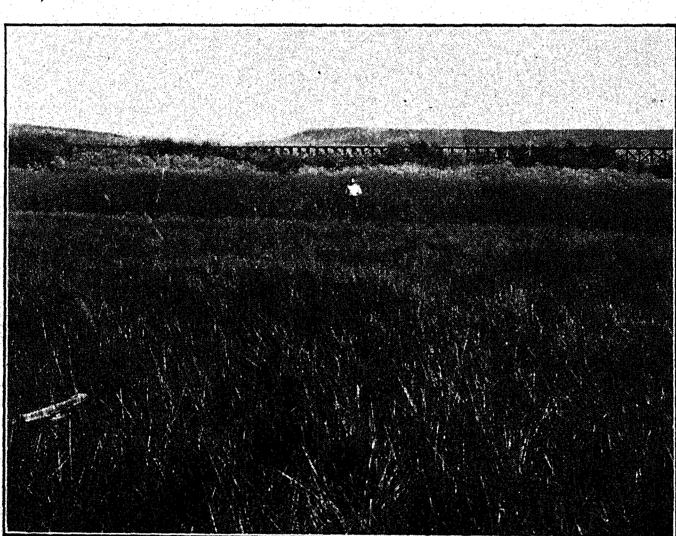

FIG. 41.—A sedge meadow of spike rush (*Eleocharis*) bordered by a bulrush or tule (*Scirpus validus*) swamp in the background.

Woodland Stage.—When the lowland has been built up to an extent where the soil is saturated perhaps only in spring and early summer, certain species of shrubs and trees may appear. Those that can tolerate

water-logged soil around their roots will be the pioneers. Various species of shrubby willows (*Salix*), dogwoods (*Cornus*), buttonbush (*Cephalanthus*), and other hydrophytic shrubs, propagating rapidly and through considerable distances by rhizomes, may form dense thickets. These, with alders (*Alnus*), tree willows, and cottonwoods (*Populus*), come to occupy more and more of the area. These woody plants react upon the habitat by producing shade and by lowering the water table both by further building up the soil and by vigorous transpiration. The drier, shaded soil is a very uncongenial place for sun-loving, sedge-meadow species, which gradually disappear, extending their territory into the zone of the receding reed swamp. Simultaneously, shade-enduring or tolerant herbs replace them, growing among the trees and shrubs.

Climax Forest.—As humus accumulates and the moist soil becomes filled with bacteria and fungi and other organisms which enrich it, many other trees may invade. Mixed forests of alder, willow, cottonwood, hackberry (*Celtis*), elm (*Ulmus*), ash (*Fraxinus*), oak (*Quercus*), and hickory (*Hicoria*) with their accompanying characteristic shrubs and herbs may result. But as the trees become denser in the drier, better aerated soil and the forest canopy more dense, many species, especially the pioneers, find difficulty in reproducing their kind since their seedlings are intolerant, *i.e.* can not grow in shade. After a few generations, only the most tolerant species may survive and a rather pure forest of oaks and hickories may develop. If the even more shade-enduring sugar maple and beech are present, they may replace the oaks. The sorting of the tree populations, however, has been no more marked than that of the herbs and shrubs. Plants of medium requirements for water (*mesophytes*) have replaced the hydrophytes. The subdominants of the climax-forest community are, moreover, all tolerant of shade. Their density, as well as their very existence, depends, in many cases, upon the control exerted upon the habitat by the dominant trees.

✓ Thus, the area once covered by deep water becomes transformed into a forest, a phenomenon clearly conceivable when one follows the actual processes of development. The various stages—submerged plant, floating plant, reed swamp, sedge meadow, woodland, and climax forest—are merely cross-sections of a continuous development made with reference to certain points where, because of more or less pure dominance, change is most apparent. This whole developmental process in action may be found about lake margins where each stage is shown as a definite zone. The stages in the present horizontal sequence from shallow water to marginal forest become arranged in a vertical sequence as the bottom of the lake is built up, forest forming the top stratum. In forests that have developed in undrained bogs where, largely because of deficient aeration the plant remains only partially decayed, borings have revealed a complets series from a forest community to submerged plants [136]

To Study the Development of a Hydrosere.—Examine the shallow water and shores of lakes, ponds, or marshes for the characteristic plants of the hydrosere. Make a list of the dominants belonging to each stage of development. Examine the roots and rhizomes of some of the floating species if possible. How do the plants adjust themselves to different depths of water? What free-floating forms have you seen? Cut sections of the leaves and stems (including rhizomes) of cattail, bulrush, and other plants of the reed-swamp stage in the field and ascertain how they are adapted to live in wet soil with a deficiency of air about the underground parts. Are the rhizomes of the various species at the same level in the soil? Can you make out whether or not the roots are much branched? Do the plants all receive light at the same level? How are they adapted for growing so close together? Are there any relict or "left-over" reed-swamp plants in the sedge-meadow stage or other indications that the area was formerly wetter? Dig into the soil and see if you can find remains of reed-swamp species. Why do the dominants of sedge meadow grow in such dense clumps? Are they also adapted to grow in wet soil? Trace the succession from the wet meadow to the climax stage. The water level should be determined by digging holes in the soil occupied by the early medial stages, and the water content determined in each zone (p. 185).

A XEROSERE

Successions initiated on bare rock, wind-blown sand, rocky talus slopes, or other situations where there is an extreme deficiency of water are termed *xerarch*, and the different stages of development constitute a xerosere. A xerosere occurring in the same climatic climax as a hydrosere will end in a similar mesophytic community.

Crustose-lichen Stage.—On the smooth surface of a bare rock, regardless of its kind, few plants are able to become established owing to the extreme deficiency of water and nutrients, great exposure to the sun, and extremes of temperature to which they are subjected. Crustose lichens alone are usually able to grow in such situations. They flourish during periods of wet weather and remain in a state of desiccation for very long periods during drought. The fungus living parasitically upon the enmeshed terrestrial algæ secures its carbohydrates from the host which, in turn, is protected by the crust-like fungus growth from extreme drought.

The rapidity with which these sponge-like organisms absorb water from rains as well as the large amount they can retain may be shown by dropping water upon them from a pipette. Mineral nutrients are obtained by the secretion of carbon dioxide which with water forms a weak acid that slowly eats into the rock into which the rhizoids sometimes penetrate for a distance of several millimeters. Nitrogen is brought in by rain or by wind-blown dust. Thus, all the life requirements of these simple, crust-like species are met.

Migration on to distant rocks takes place either by wind-carried spores or lichen fragmentation, *i.e. soredia.* Thus, species of *Rhizocarpon, Lecidea, Rinodina,* and *Lecanora* come to colonize these bare

areas and play an important part in converting the rock into soil. Not only do they exert an influence at the contact of thallus and rock, but also the corroding effect of carbonic acid and perhaps other secretions extends beyond the thallus margins during moist weather. This permits slow extension of the thalli or furnishes starting places for new ones (Fig. 42). Thus, lichens help corrode and decompose the rock, supplementing the other forces of weathering, and by mixing the rock particles with their own remains make conditions possible for the growth of other vegetation. The rapidity with which a minute amount of soil will form is controlled very largely both by the nature of the rock and by the

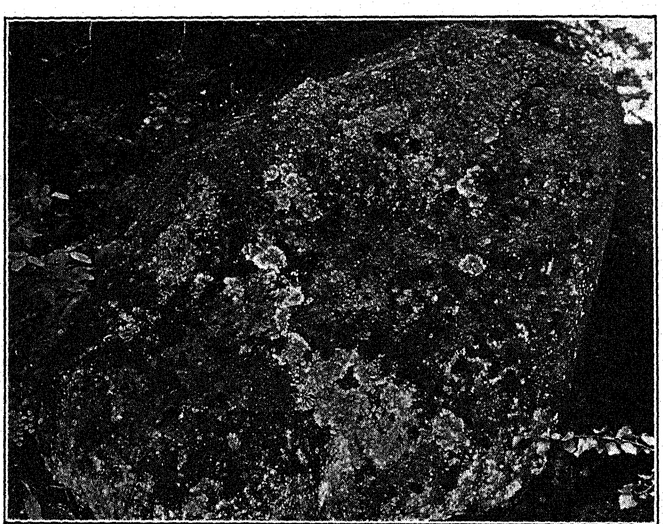

FIG. 42.—Lichens and mosses on a granite boulder, showing the early stages of a xerosere.

climate.[169] On quartzite or basalt in a dry climate, the crustose-lichen stage might persist for hundreds of years.[115] But on limestone or sandstone in a moist climate, sufficient change to permit the invasion of foliose lichens may occur within a lifetime.

Foliose-lichen Stage.—Foliose lichens, *i.e.* those attached to the substratum at a single point or along a single margin, appear as soon as a little soil has accumulated (Fig. 43). On the more weathered portions of the rock and in depressions or other slightly less exposed situations, they slowly replace the crustose forms. Their expanding leaf-like thalli may completely overshadow the latter. Thus, cut off from the source of light, the crustose species may die and decay. About the foliaceous invaders, water has a better chance to collect and to be absorbed, evaporation is greatly decreased, wind-and water-borne lichen fragments and dust particles lodge, and humus is more rapidly accumulated because of its less rapid oxidation. The acids produced by the living and decaying

plants are constantly eating farther into the rocks. Indeed, it is probable that the change from crustose to foliose lichens is a change of habitat as great as happens anywhere in the sere, although too minute in extent to be impressive. After the crustose forms give way to various foliose species (such as *Dermatocarpon*, *Parmelia*, *Umbilicaria*, and others), a new type of invader appears.[160]

FIG. 43.—A foliose lichen (*Gyrophora*) growing on a rock. (*Photo by Fink.*)

Moss Stage.—As soon as sufficient amounts of soil have accumulated in the minute crevices and depressions in the rock, xerophytic mosses begin to appear. These are commonly species of black moss (*Grimmia*), hair moss (*Polytrichum juniperinum*, *P. piliferum*, *P. commune*), and twisted moss (*Tortula*). They may have migrated long distances by wind-blown spores. Their rhizoids compete with those of the foliose lichens for water and nutrients and the erect stems often exceed the latter in height. The power of withstanding desiccation is almost as marked among these pioneers as among the lichens. They and the more exacting foliose species may occur simultaneously, or, indeed, the mosses may sometime precede foliose lichens.[109]

Soil rapidly accumulates among the erect stems as the plants dying below but continuing growth above build up the substratum and constantly increase their area. The depth of soil under the cushion-like moss mats, often an inch or more, contrasted to the thinner layer under the foliose lichens, and the hard substratum under the crustose forms can best be realized by inserting a knife blade into a rock surface occupied

by each. Sometimes, fruticose lichens, especially *Cladonia* and *Stereocaulon*, with the mosses overtop the foliose forms which are unable successfully to compete with the invaders. At the same time that they yield to the mosses, they more completely invade the area of the crustose forms. Frequently, all three stages may be found on a single rock surface, the pioneers occupying the most exposed places.

Herbaceous Stage.—The soil-forming and soil-holding reactions of the mosses are so pronounced that the seeds of various xerophytic herbs, especially short-lived annuals, are soon able to germinate and the plants to mature, although the first generations, because of the drought and sterility of the soil, may make only a stunted growth. Their roots

FIG. 44.—Early herbaceous stage of a xerosere. The plants growing in the shallow, rocky soil are a drought-enduring bluegrass (*Poa*), knotweed (*Polygonum*), and woolly plantain (*Plantago*).

continue the process of corroding the rock, and each year the humus from their decaying remains enriches the soil. Gradually, biennials and perennials begin to invade, ever increasing in numbers as the habitat becomes more congenial (Fig. 44).

The processes of rock disintegration and humus and nutrient accumulations are greatly accelerated as the tangled network of roots increases and the soil becomes shaded. Evaporation and temperature extremes are decreased, humidity slightly increased, and drought periods shortened. The bacterial, fungal, and animal populations of the soil increase and conditions gradually become less xeric. The intensely xerophilous, shallow-rooted wire grass, poverty grass, and dwarfed specimens of bluegrass (species of *Aristida*, *Festuca*, and *Poa*) with mullein (*Verbascum*), alumroot (*Heuchera*), and rock ferns are supplemented in their invasion

by many drought-enduring mustards, cinquefoils (*Potentilla*), goldenrods (*Solidago*), and many others. The reactions brought about by the new community, especially the reduced light, are distinctly detrimental to the mosses and fruticose lichens which gradually become fewer in number.

Shrub Stage.—On the soil thus prepared by the pioneer lichens, mosses, and herbs, woody plants find conditions possible for growth. Shrubs may start from seed or invade from adjacent areas by rhizomes. In such invasions, snowberries (*Symphoricarpos*), sumac and poison ivy (species of *Rhus*), and ninebark (*Physocarpus*) often dominate. Thickets of leafy shoots from the underground tangle of rhizomes overtop and shade the herbs and, when the shrubby growth becomes sufficiently dense, the former possessors of the land find the habitat so modified that growth becomes almost or quite impossible. The herbaceous population largely disappears. Among the numerous stems, the falling leaves find lodgement and wind-blown snow accumulates. Massive networks of roots fill the soil. The deepest of these continually corrode the rocks and pry open their pores and crevices. Wind movement is retarded and humidity is higher above the decaying leaf mold covering the shaded soil, from which surface evaporation is greatly reduced. All these conditions, coupled with the enriched soil with its greater capacity for holding water, furnish an excellent nursery for tree seedlings, and trees may now begin to appear.

Climax Forest.—The first species of trees are relatively xeric. The pioneers are widely spaced, and the hard conditions of life are reflected in their stunted growth. But as weathering processes continue and the soil deepens, trees increase both in number and vigor. A forest of bur oak and bitternut hickory may develop. With increasing shade, the light-demanding shrubs fail and other more tolerant and mesophytic ones replace them under the protection of the leafy tree canopy. A new herbaceous vegetation develops in the forest shade, indicating a more humid atmosphere and a moister and richer soil than had heretofore prevailed. This is quite in contrast to the once bare rocks.

The accumulated mold of generations of forests worked over by an ever increasing host of soil organisms furnishes a more constantly moist soil and other conditions favorable to a more mesophytic forest. The bur oak-bitternut hickory associes may be replaced by the red oak-shellbark hickory association. Once established, the invaders become controlling. Their shade is so dense that the bur-oak and bitternut-hickory seedlings grow poorly or die. Only tolerant species, such as ironwood (*Ostrya*) and elms (*Ulmus*), can live in this community. Once more the shrubby and herbaceous populations shift, the less tolerant following the former community in its invasion of the shrubs. The most tolerant, supplemented by other invading mesophytes, constitute the layers of the climax mesophytic forest.

To Study the Development of a Xerosere.—Examine the development of vegetation on a rocky ledge or other outcrop or on very thin, stony soil, etc. Determine the power of the crustose lichens to absorb and hold water when it is dropped upon them. Is there any evidence that they are increasing their area of occupation? Find places where foliose lichens are replacing them. By scratching the rock with a knife blade, determine the depth of loosened materials under crustose and foliose lichens and under xeric mosses that have replaced them. Determine the power of the cushion of moss to absorb and hold water. What parts of the moss plants are alive? Where do the pioneer herbs first appear? Make a list of some of the most important ones. Does the sere end in grassland or is there a shrub stage? What are the most important shrubs? How do they propagate? Examine their underground parts in relation to the underlying rock. Trace the succession to the climax of the region. Determine the water content in each stage of the sere where sufficient soil occurs to afford representative samples, discarding all large rock particles.

Summary of Succession.—In both hydrosere and xerosere, the habitat has changed from one of extreme to one of medium water relations, and the vegetation, at first adapted to hydric and xeric conditions, respectively, has developed into a mesophytic forest. This process may be summarized as follows:

Hydrosere		MAPLE-BEECH (ACER- RED OAK-SHELLBARK HICKORY RED OAK (QUERCUS SHELLBARK HICKORY (HICORIA
Elm-ash (*Ulmus-Fraxinus*)		Associes
Ash (*Fraxinus*)	Consocies	
Walnut (*Juglans*)	Consocies	
Elm (*Ulmus*)	Consocies	
Willow-cottonwood (*Salix-Populus*)		Associes
Cottonwood (*Populus*)	Consocies	
Alder (*Alnus*)	Consocies	
Willow (*Salix*)	Consocies	
Spike rush-sedge (*Eleocharis-Carex*)		Associes
Sedge (*Carex*)	Consocies	
Rush (*Juncus*)	Consocies	
Spike rush (*Eleocharis*)	Consocies	
Bulrush-cattail (*Scirpus-Typha*)		Associes
Cattail (*Typha*)	Consocies	
Reed (*Phragmites*)	Consocies	
Bulrush (*Scirpus*)	Consocies	
Water lily-pondweed (*Nymphæa-Potamogeton*)		Associes
Pondweed (*Potamogeton*)	Consocies	
Smartweed (*Polygonum*)	Consocies	
Water lily (*Nymphæa*)	Consocies	
Water lily (*Castalia*)	Consocies	
Water weed-water milfoil (*Elodea-Myriophyllum*)		Associes
Water milfoil (*Myriophyllum*)	Consocies	
Pondweed (*Potamogeton*)	Consocies	
Water weed (*Elodea*)	Consocies	

FURTHER STUDIES OF SUCCESSION

In the preceding paragraphs the outlines of processes that require long periods of time for their completion have been sketched, the successions on rocks usually being longer than those in water. Moreover, only two typical successions have been outlined. Others occurring in sand, in bogs, and elsewhere will now be considered together with certain other phenomena fundamental to an understanding of this developmental process.

Viewpoints of Succession.—The successive waves of plant populations—crustose lichens, foliose lichens, mosses, herbs, shrubs, and trees—each, in turn, holds possession of a habitat and produces its profound influences upon it. Beginning slowly, increasing to a maximum, and then gradually receding, the plant populations of each have made conditions fit for the next community but often less fit for their own continuation. This is true for both hydrosere and xerosere. This is one viewpoint of succession. The process may also be viewed as a change of life-forms or phyads,[172,500] the lichen phyad being replaced by the higher type of moss life-form, and this by the herb, shrub, and tree in regular sequence. Fixing attention on the changes in the habitat,

FAGUS) FORMATION
(QUERCUS-HICORIA) ASSOCIATION — Xerosere
RUBRA) CONSOCIATION
OVATA) CONSOCIATION

Bur oak-bitternut hickory (*Quercus-Hicoria*)		Associes
Bitternut hickory (*Hicoria*)	Consocies	
Bur oak (*Quercus*)	Consocies	
Sumac-snowberry (*Rhus-Symphoricarpos*)		Associes
Snowberry (*Symphoricarpos*)	Consocies	
Ninebark (*Physocarpus*)	Consocies	
Sumac (*Rhus*)	Consocies	
Wire grass-proverty grass (*Aristida-Festuca*)		Associes
Poverty grass (*Festuca*)	Consocies	
Woolly plantain (*Plantago*)	Consocies	
Cinquefoil (*Potentilla*)	Consocies	
Wire grass (*Aristida*)	Consocies	
Black moss-hair moss (*Grimmia-Polytrichum*)		Associes
Hair moss (*Polytrichum*)	Consocies	
Twisted moss (*Tortula*)	Consocies	
Black moss (*Grimmia*)	Consocies	
Foliose lichen (*Cladonia-Gyrophora*)		Associes
Gyrophora	Consocies	
Parmelia	Consocies	
Cladonia	Consocies	
Crustose lichen (*Rhizocarpon-Lecanora*)		Associes
Lecanora	Consocies	
Rinodina	Consocies	
Lecidea	Consocies	
Rhizocarpon	Consocies	

one finds the rock becoming less and less dry, the lake area with a diminishing water content, both approaching the medium condition of mesophytism. A study of vegetation as a developing organism comprehends all three points of view in a connected whole.

Other Successions on Rock.—Xeroseres do not always occur in the exact sequence described. On talus slopes, for example, the interstices between the coarse, loose rock fragments may furnish a habitat in which the seeds of herbs or even shrubs or trees may germinate and the seedlings successfully ecize (*i.e.* make a home). This happens long before the lichens and mosses on the rock surfaces have had sufficient

FIG. 45.—Succession on a gravel slide in the Rocky Mountains. The most important species are a parsley (*Pseudocymopterus*) and a borage (*Krynitzkia*) in the foreground.

time to form even a thin soil. The rapidity of colonization and development, aside from climate, depends, in part, upon the nature and degree of the physical and chemical erosion of the rock fragments and partly upon how much humus is carried down by the rain from the decaying surface vegetation. On a talus slope composed of fine gravel intermixed with coarse sand, succession is rapid.

Herbs usually play the pioneer rôle, binding the loose soil, forming mats on its surface, adding humus, and otherwise producing a suitable habitat for shrubs and trees (Fig. 45). Vast areas in the mountains are regularly forested in this way, gravel slide with its sparsely placed herbs giving way to grass- and herb-covered half-gravel slide into which shrubs invade only to be replaced later by forests of pine, fir, spruce, etc., depending upon climatic control.

A shrub or heath consocies may result from several types or lines of succession which converge into it. Not infrequently, while crustose and foliose lichens are aiding in weathering the rock surface, fruticose lichens, mosses, and crevice herbs are forming humus in the clefts of the rock, while in depressions on the same rock mass, where water stands part of the time, mats of sedges, etc., may flourish and similarly build up soil. Finally, the shrub vegetation of the rock surface coalesces with that of the crevices. The rock pool also adds its quota, mostly of similar species, all forming a dense mat of shrubby vegetation quite covering the rocky substratum[110] (Fig. 46).

FIG. 46.—A falling tree exposing the substratum of boulders upon which vegetation has laid a deep blanket, part of which is now a living mat of moss. (*Photo by W. L. Bray.*)

Successions in Sand.—Extensive successional studies have been made on the sand dunes about Lake Michigan.[122,171] The prevailing westerly winds blow the beach sand into dunes which almost continuously fringe the eastern and southern borders of the lake. The vegetation, at first extremely xeric, culminates in a mesic maple-beech forest.

Extensive beach dunes can not be formed, since one wind destroys what another builds, unless the plants, which are obstacles compelling the wind from the lake to deposit its load, continually increase in size. Such plants must be pronounced xerophytes or be able to endure partial burial by the sand or continue to thrive when much of the sand has blown away and the underground parts are partially exposed.

Embryonic Dunes.—The most successful dune formers are marram grass (*Ammophila*), wheat grass (*Agropyron*), sand reed (*Calamovilfa*),

willows (*Salix*), sand cherry (*Prunus*), and cottonwoods (*Populus*). All have great powers of vertical elongation as the sand piles up about them and some of the grasses and shrubs propagate extensively by rhizomes which, with the tangle of roots, bind the sand. The dunes may reach a height of 10 feet or more (Fig. 47).

In low places where the wind blows the sand away to near the water level, cottonwoods may germinate and grow rapidly forming a new obstacle for the wind-blown soil. No vegetative propagation takes place nor can new individuals start in the dry sand. Cottonwood dunes are consequently the highest and steepest. The trees may become almost buried but are still able to survive.

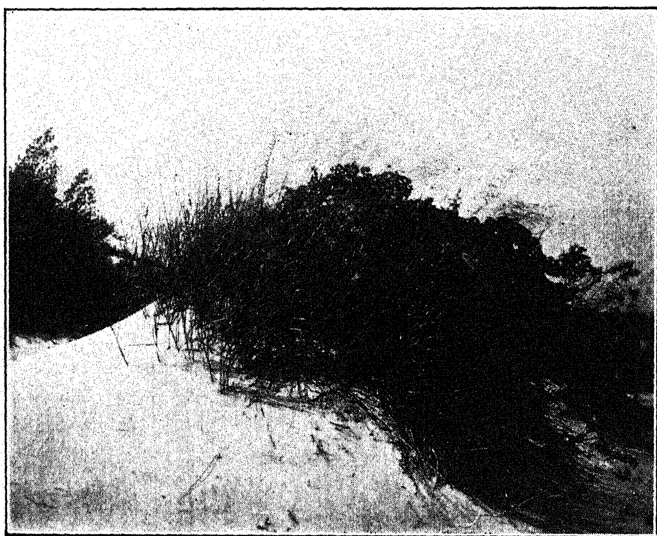

FIG. 47.—An embryonic dune with the sand reed (*Calamovilfa longifolia*) holding the sand. (*Photo by Geo. D. Fuller.*)

Wandering Dunes.—As the embryonic dunes become larger and higher, conditions for sand accumulation become more favorable. But the dune-holding plants have grown farther from the water level each year. Cottonwoods are relatively short-lived and no new trees can replace the old ones, once the dune is formed. Gradually, the wind begins to reshape the dune, the plants lose their hold, and the dune begins to wander. The wind blows the loosened sand into great dunes or series of dunes which have a long, gentle slope toward the lake but a steep leeward side. It sweeps up the windward slope carrying or rolling the sand along until the crest is reached, when the sand rolls down the leeward side. The crest of dunes is often higher than the forests over which they may slowly but irresistably advance (Fig. 48). They move

forward only a few inches or, at most, a few feet each year but always forward.[125] The old vegetation is entirely covered, but as the dunes advance the remains of buried forests may be uncovered.

Arrested Dunes.—Vegetation appears to be unable to capture a rapidly moving dune, although xerophytes may grow upon it. But as the dune wanders farther from the lake, perhaps a mile or more, the force of the wind is decreased, usually by other dunes being built up between it and the beach. Vegetation commonly gets its first foothold at the base of the lee slope about the outer margin of the dune or dune complex. Here there are abundant soil moisture and protection from the wind. Plants may creep up the slope by vegetative propagation. Marram grass

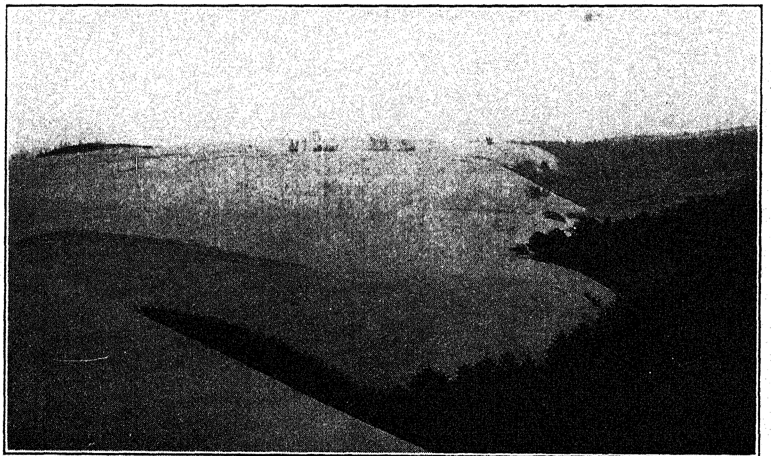

FIG. 48.—Advance of a dune over forest and swamp, Dune Park, Indiana. (*Photo by Geo. D. Fuller.*)

and other xeric pioneers are among the first to appear. They are followed by a dense growth of shrubs, dogwood (*Cornus*), willows (*Salix*), choke-cherry (*Prunus*), and grape (*Vitis*). A mesophytic forest dominated by linden (*Tilia*) rapidly replaces the shrubs but is, in turn, replaced by the climax maple and beech.

On the long windward slopes, which make up about nine-tenths of the dune area, the succession is quite different, probably owing to the action of the drying winds. The pioneer herbs of the embryonic dunes, many of which grow on the shifting dune complex, are succeeded by a shrub stage, consisting largely of xeric evergreens especially shrubby and prostrate junipers (*Juniperus*) and bearberry (*Arctostaphylos*). Conditions become less severe under cover of the shrubs, and a coniferous forest develops. Jack pine (*Pinus banksiana*) is usually the first tree to appear. It may be followed by red pine (*P. resinosa*) or the latter may be the pioneer where the jack pine is absent. They are succeeded by

climax forests of white pine (*P. strobus*) in the Great Lakes forest formation. In the deciduous forest climax the white pines are replaced by oaks. Black oak (*Quercus velutina*) commonly appears first, but it is succeeded by forests of white oak (*Q. alba*). Finally, the sere culminates in a maple-beech climax.

Succession on River Bars.—When sand or silt is deposited in a river as bars or islands, colonization and succession usually occur rapidly. This is due to relatively favorable soil. Trees with light, wind-blown seeds or fruits, such as willows and cottonwoods, are often the pioneers. These are regularly followed, if the island is built up, by more tolerant species such as elms, ashes, linden, etc., in the development toward the climax forest.[163]

Succession in Bogs.—The hydrosere in bogs is different from that in ponds and lakes. A bog is an area of wet, porous land of which the soil is composed principally of partially decayed vegetable matter so loosely consolidated and containing so much water that the surface often shakes or quakes when one walks on it.[136] Bogs are different from ponds and lakes in being undrained. This results in deficient aeration and the concomitant conditions of a poor bacterial and fungus flora and, often, of acidity. Bogs are most abundant in the glaciated portions of the north temperate zone where precipitation is great and regularly distributed, evaporation low, run-off small due to undrained glacial basins, and where a rather long summer season affords conditions conducive to vigorous growth.[183,309]

The earlier stages of submerged and floating plants may be quite the same as for ordinary swamps, but medial and later stages are different. Instead of a process of filling up the depression, the bog is usually bridged over with a mat of vegetation which culminates in a forest. The third stage in development usually consists of a floating sedge mat which grows inward from the periphery of the bog over the open water. This is composed of various sedges, *e.g. Carex filiformis*, rushes, etc., usually with much-branched, light, buoyant rootstocks. A tangle of roots arises from the nodes and extends into the water. Each year the mat extends farther outward, as new shoots grow from rhizome tips, and its older parts increase in thickness. Where the floating mat has reached a thickness of 18 to 24 inches, it may even support the weight of a man. Sometimes the water willow (*Decodon*) plays a similar rôle.

Various mosses, especially peat mosses (*Sphagnum*), find excellent conditions for growth about the moist tufts of sedges, etc. They retain water like an enormous sponge, dying below and growing above. Numerous shrubs such as cranberries (*Vaccinium*), leather leaf (*Chamaedaphne*), Labrador tea (*Ledum*), poison sumac (*Rhus*), and bog rosemary (*Andromeda*) are characteristic of the subsequent stage. These are accompanied by numerous herbaceous species among which are pitcher

plants (*Sarracenia*), sundews (*Drosera*), orchids, various ferns, buckbean (*Menyanthes*), and many others.

Succeeding the shrubs are characteristic swamp trees such as tamarack (*Larix laricina*), black spruce (*Picea mariana*), and white cedar (*Thuja occidentalis*). In the Great Lakes forest, white pine is the climax stage (Fig. 49).[63,132]

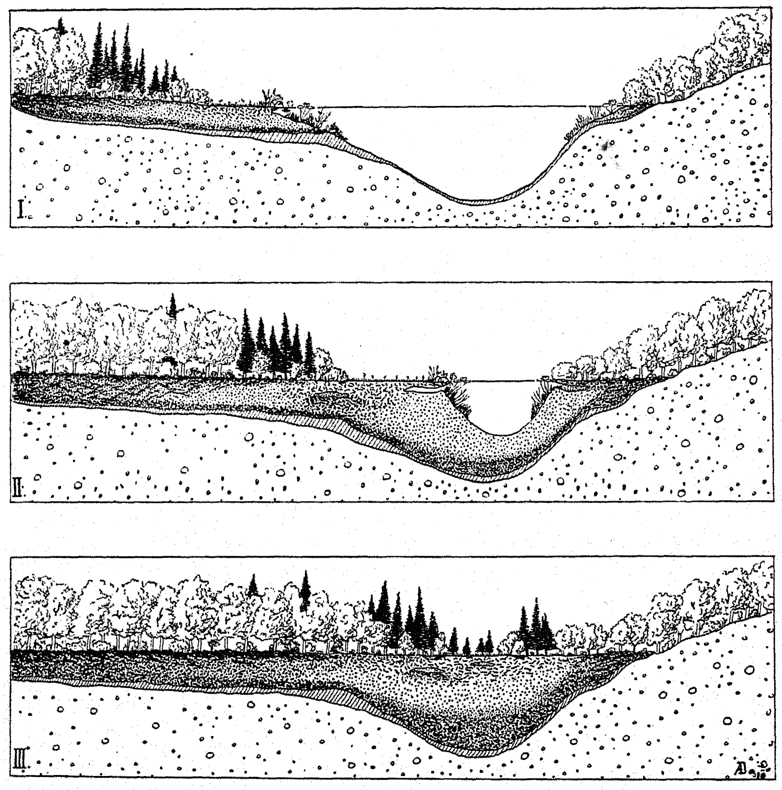

FIG. 49.—Diagram illustrating stages in the origin of peat deposits in lakes from open water with submerged plants to the climax forest. (*After Dachnowski. Reproduced by permission from Geological Survey of Ohio, Bull.* 16.)

Variation in Stages and Dominants.—A study of succession in many lakes and ponds or on numerous rock outcrops, etc., shows that variations occur in the number of stages as well as in the dominants of a given stage.[89] In the seres just outlined, the usual stages have been described and representative dominants have been used to illustrate each stage. Some reed swamps may be entirely dominated by wild rice (*Zizania*), just as certain rock ledges may be clothed with a xeric herbaceous vegetation that may include none of the preceding consocies. But

the general sequence of stages is the same whether the succession occurs in Maine or in New Mexico.

Seres on primary areas, *i.e.* those previously unoccupied by plants, are designated as primary or *priseres;* those on secondary areas such as lumbered, burned, flooded, or otherwise denuded ones are termed *subseres.* Since soil is already formed in subseres and germules usually on the ground, succession nearly always takes place much more rapidly. Usually, only the middle (medial) and final stages need be repeated. Succession after lumbering in a deciduous forest may consist simply of a shrub stage followed by the climax forest which has reproduced by sprouts from the bases of the stumps. In burned, coniferous forest, a liverwort-moss stage may be quickly replaced by one of herbs and this, in turn, after only 2 or 3 years, by shrubs, which are soon followed by trees. Thus, the number of stages varies greatly. In subseres there may be only 3 or 4 or fewer. Among priseres, the number is usually greater, sometimes 10 or more.

The initial stages of primary seres are marked by extreme physical conditions and by correspondingly specialized life-forms. Such primary areas as open water, rock, dune sand, etc., occur throughout the world. The life-forms produced by them are likewise universal and are usually highly mobile. Consequently, the pioneer aquatics of water areas, the lichens and mosses of rocks, the xeric grasses of dunes, and the halophytes of salt areas consist of much the same species throughout the Northern Hemisphere. Hence, the initial stages of water, rock, dune, or saline seres may be nearly or quite identical in widely separated regions. Some of the medial and the final stages of each are determined by the particular climatic climax under which they occur. From the extreme nature of primary areas and the plants in them, initial stages persist for a long time, largely because of the slowness of reaction and the incomplete occupation. Primary areas differ much in these two respects. The greatest duration is found in the initial stages of a rock sere. The stages of a water sere follow each other more rapidly, and those of a dune still more rapidly, though the extent of the area in both cases plays a part.

- Prisere
  - Hydrosere
    - Halosere
    - Oxysere
  - Xerosere
    - Lithosere
    - Psammosere
- Subsere
  - Hydrosere
  - Xerosere

Classification of Seres.—Seres are classified primarily upon the water content of the initial area in which they develop. With priseres, the extremes are marked and the quality of the water content also frequently becomes controlling. Consequently, hydroseres in saline areas are distinguished as (salt) *haloseres* and those in acid soils as (acid) *oxyseres.* Moreover, while the surface of rocks and of dune sand may be almost equally dry, the differences of hardness and stability result in very dissimilar seres. These are distinguished as (rock) *lithoseres* and (sand) *psammoseres,*

respectively. In the case of subseres, extreme conditions of water content are rare or they persist for a brief period only (Fig. 50). Hence, it is sufficient to recognize but two subdivisions, hydrosere and xerosere.

The Climax.—Developmental processes have been going on for so long a time that on soils long formed the major portions of the area are usually covered with the stabilized or climax vegetation. The initial and medial stages of succession may not be much in evidence. But they are found everywhere in sufficient abundance to give the complete story of the way in which vegetation has helped reduce into soil the solid rock of mountains, emerged ocean margins, or glacier-swept areas.

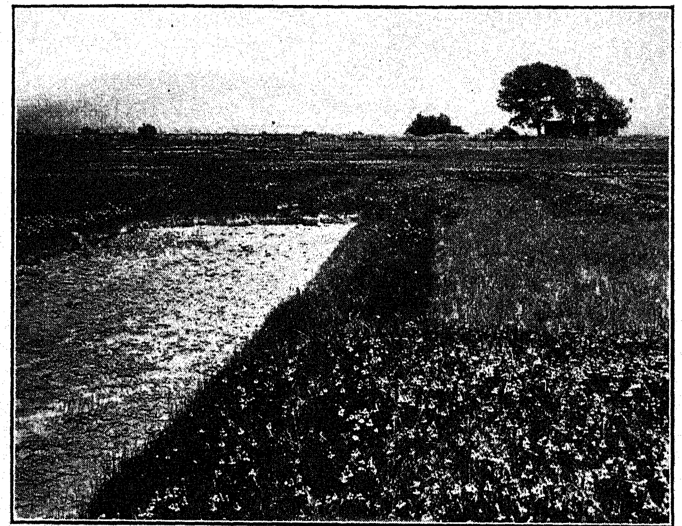

FIG. 50.—Subsere alternes in New Mexico due to the removal of sod for adobe houses, showing three stages of a subsere.

In the rocky wastes of the mountains, on eroding cliffs and gravel-strewn talus slopes, this story is most vividly portrayed. The building of ponds, lakes, lagoons, and marshes into dry land, just as it is taking place today, has occurred on an enormous scale in the past. This is shown by accumulations of peat and earth-covered seams of coal.

While the general sequence of a sere is the same nearly everywhere, the degree to which it can develop, that is, the climax community in which it ultimately terminates, is determined by the climate. Had the hydrosere described (p. 55) occurred in the grassland climax of Dakota or Kansas, shrub and woodland communities would have been eliminated and the sedge-meadow stage would have given way to prairie. In the Pacific Coast forest climax, the xerosere would have passed from the shrub stage to one of yellow pine (*Pinus ponderosa*) followed by Douglas

fir (*Pseudotsuga*) and tamarack (*Larix*) and possibly culminated ultimately in a forest of white cedar (*Thuja*) and hemlock (*Tsuga*).

Subclimaxes.—Every complete sere ends in a climax when a point is reached where the occupation and reaction of the dominants or dominant are such as to exclude invasion by another dominant. Frequently, however, the climatic climax is not developed on all areas within the climatic control. The development of the vegetation may be arrested at some stage of the succession due to repeated burning, cutting, grazing, flooding, and other causes. This imperfect stage of development, in which the vegetation is held indefinitely either by natural or by artificial factors, is termed a *subclimax*.

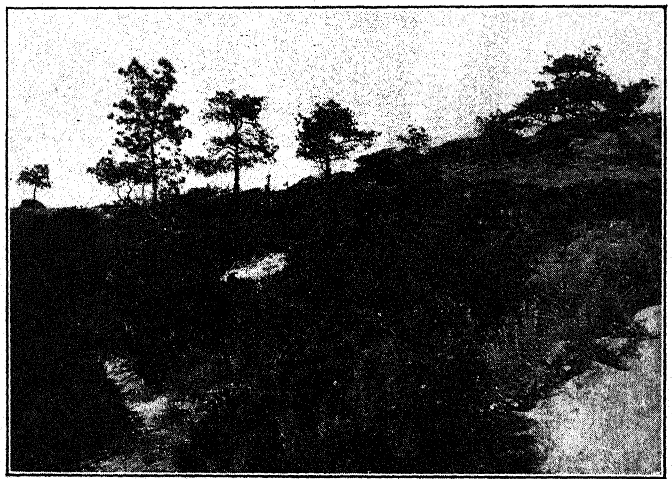

FIG. 51.—Chaparral subclimax in California due to fire. The pines are relics of a former forest.

Grassland areas are produced the world over as a result of burning and grazing combined, and they persist just as long as burning recurs.[103] Woodland is frequently reduced to scrub by fire, and the scrub often persists wherever repeated fires occur (Fig. 51). Even when fires cease after the settlement of a region, grassland and scrub climaxes persist for a long time because of the more or less complete removal of the forest.[33,34]

The range lands of the Wasatch Mountains in Utah pass through various stages of development, which culminate in a cover of wheat grasses (*Agropyron*) constituting a *subclimax herbaceous stage*. Coniferous forest constitutes the true climax. When the cover of wheat grasses, which have formed a turf excluding most other plants, is broken by destructive grazing or otherwise, both deep-rooted and shallow-rooted species can successfully invade. Thus the yellowbrush-needle grass (*Chrysothamnus-Stipa*), which constitutes the *mixed grass and weed stage*, becomes established. Where the turf-forming wheat grass is

permitted to redevelop, it again completely occupies the area, entirely replacing the yellowbrush and needle grass. So completely do the roots occupy the soil that practically all of the water is absorbed in the surface foot, and deeper rooted plants die. On the bunch type of wheat-grass land they may persist as subdominants.

Further overgrazing of the yellowbrush-porcupine grass associes, which includes considerable bluegrass (*Poa*), fescue grasses (*Festuca*), and scattered stands of the relict wheat grasses, causes the invasion by a still earlier stage. This is characterized by brome grasses (*Bromus*), beardtongue (*Pentstemon*), sagewort (*Artemisia*), yarrow (*Achillea*), etc., and is designated as the *second or late-weed stage.* These invaders are turf-forming perennial weeds. Associated with them are various short-lived, perennial herbs, many of which propagate only by seed. Continued heavy grazing, which not only destroys the perennials but also permits soil erosion, depletion of humus, and heavy leaching of nutrients, results in a very open plant cover largely consisting of annual weeds. Thus, the *first or early-weed stage* characterized by lamb's quarters (*Chenopodium*), tansy mustard (*Sophia*), knotgrass (*Polygonum*), etc., replaces the second or late-weed stage.

By judicious range management the subclimax wheat-grass consocies, which is especially well suited to the grazing of cattle and horses, may be indefinitely maintained. Slight overgrazing produces the highest type of development of the mixed-grass and weed stage which, because of its large variety of palatable plants, is probably the most desirable, all classes of stock considered, and especially for sheep. Thus, the intensity of grazing determines the subclimax stage of development. The principle is applicable to pasture lands generally.[436]

The subclimax prairie covering the region between the deciduous forest and the true prairie has never developed into a true chaparral or forest climax because of fires, mowing, grazing, and other causes. It is obvious that any forest may be held in a desired stage of development by selective cutting. Recurrent fires in many parts of the Rocky Mountains have held the forest successions in the lodgepole-pine stage of development. Fires in the Cascade Mountains have greatly favored the Douglas fir, the most important lumber tree, and indefinitely delayed the development of a cedar-hemlock climax. In parts of New England, forest and scrub land are burned regularly to promote the development of the blueberry-shrub stage, the latter being commercially more valuable than the trees.[367]

Repeated flooding of lowlands makes conditions favorable for the growth of wild rice (*Zizania*) and many other hydric plants which furnish excellent food for wild ducks, geese, and other game. In a similar manner, cranberry swamps may be held in a shrub or heath subclimax. While the course of development may be interrupted or deflected, slowed

or hastened, or even stayed for a long period, whenever movement does occur, it is always in the direction of the climax.

Postclimaxes.—Local communities may develop or persist where especially favorable conditions of soil, humidity, etc., exist, which represent a more highly developed stage than the present climatic climax of the region. Forests along streams in grassland or sagebrush desert are illustrative (Fig. 52). Many low, rocky ridges and buttes extending from mountainous areas into grassland are frequently pine clad on their

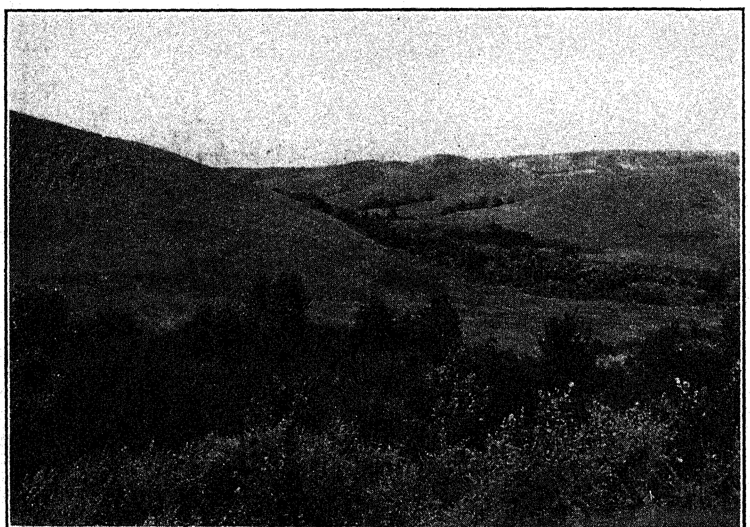

FIG. 52.—Postclimax of scrub and woodland in the prairie climax in North Dakota. The shrubs are buffalo berry and service berry; the trees, elm, ash, and bur oak.

crests, the sides are flanked with shrubs, and the valleys and lower slopes sodded with grasses. The thin soil underlaid with creviced rocks is favorable to an open growth of pines, since the grasses do not grow well and, hence, compete little for water. But as soil is formed, both trees and shrubs finally fail to reproduce in the increasingly dense herbaceous cover. In the competition for water, grasses dominate in this grassland climate.

A Study of Other Types of Succession.—If access can be had to gravel slides, sand dunes, river bars, bogs, etc., the successions should be worked out as fully as time permits. Subseres should also be studied. These may be found, at least in miniature, almost anywhere in disturbed places.

CHAPTER V

INITIAL CAUSES OF SUCCESSION

Having gained a general view of succession, the universal process by which formations develop, the causes may now be studied somewhat in detail. The development of a climax formation consists of several essential processes. Every sere must be initiated and its life-forms and species selected. It must progress from one stage to another and finally must terminate in the highest stage possible under the climatic conditions present. Since succession is a series of complex processes, it follows that there can be no single cause for a particular sere.

The processes causing succession may be distinguished as initiating or *initial causes*, continuing or *ecesic causes*, and stabilizing or *climatic causes*. Initial causes produce the bare area or destroy the original population in areas already vegetated. The deposition of sediment as alluvial fans at the mouth of a river illustrates the former; and the wandering sand dune covering a forest, the latter. Ecesic causes produce the essential character of vegetational development, *i.e.* the successive waves of plant populations. They have to do with the interaction of vegetation and habitat and are directive in the highest degree. Climatic causes determine the nature of the climatic climax, that is, where the succession will end. They likewise have a profound effect in determining the population from beginning to end, the number and kinds of stages, as well as the reactions of the successive stages. While the process of succession in the tropics is similar to that in temperate regions, the plant populations are often very different. Clearly this is due to climate.

INITIAL CAUSES

Initial causes of succession are those which produce a new or denuded soil upon which invasion is possible. Seres originate only in bare areas or in those in which the original population is partially or wholly destroyed. It is a universal law that in all bare places new communities arise, except in areas which present the most extreme conditions of water, temperature, light, or soil. Of these there are few. Even fields of ice and snow show algal pioneers, rocks in the driest deserts bear lichens, caves contain fungi, and all but the saltiest soils permit the entrance of halophytes. From the standpoint of succession, water is the most important of bare habitats, and it is almost never too extreme for plant life. Seaweeds grow and fruit abundantly in Arctic waters at

temperatures of about 32°F., and various algæ invade hot springs where the temperatures are as high as 180°.

Habitats are either originally bare or bare by denudation. The former are illustrated by water, land produced by rapid emergence, such as islands, continental borders, etc., lava flows, deltas, and dunes. Denuded habitats arise in the most varied ways and are best exemplified by bad lands, flooded areas, burns, and fallow fields. The essential difference between the two is that the originally bare area has never borne a plant community and is, therefore, physically different in lacking the effects of reactions caused by successive plant populations. Not only must the initiating process produce a new area capable of ecesis but it must also furnish it with physical factors essentially different in quantity at least from the adjacent area. Otherwise, the new area would quickly be controlled by the association at hand and soon made an intrinsic part of it.

Treated from the standpoint of the nature of the agent or process producing bare areas, the causes may be grouped as *topographic*, *e.g.* erosion and deposit; *climatic*, *e.g.* wind, fires caused by lightning, etc.; and *biotic*, *i.e.* produced by man or other organisms.

Topographic Causes.—All of the forces which mold land surfaces have one of two effects. They may add to the land or take away from it. The same topographic agent may do both, as when a stream erodes in its upper course and deposits a delta at its mouth or undercuts one shore and forms a mud bank or sand bank along the other. In similar fashion, a glacier may scoop out a pond or a lake in one region and deposit the material as a moraine in another. The wind may sweep sand from a shore or blow-out and heap it up elsewhere, or it may carry dust from dry lake beds or flood plains for long distances and pile it in great masses of loess. Gravity in conjunction with weathering removes the faces of cliffs and accumulates the coarse material in talus slopes at the base.

Bare Areas Due to Erosion.—The chief topographic causes producing bare areas are erosion and deposit. Erosion is the removal of the soil or rock by the wearing away of the surface of the land. The agents of erosion are water, wind, gravity, and ice (Fig. 53).

Important areas laid bare through erosion by water are gullies, ravines, valleys, sand draws, washes, flood plains, river islands, banks, lake shores, crests and slopes, and bad lands and buttes. In all, the success of initial invasion depends upon the kind of surface laid bare and the water content as determined by the surface, the slope, and the climate of the region. The form and nature of the area itself are unimportant except as they affect these factors.

Characteristic bare areas due to wind erosion are dunes and sandhills, particularly the blow-outs. Related to these are the strands from which

the dune sand is gathered by the wind, and the plains of rivers, lakes, and glacial margins from which sandhills and loess deposits have been formed by wind action.

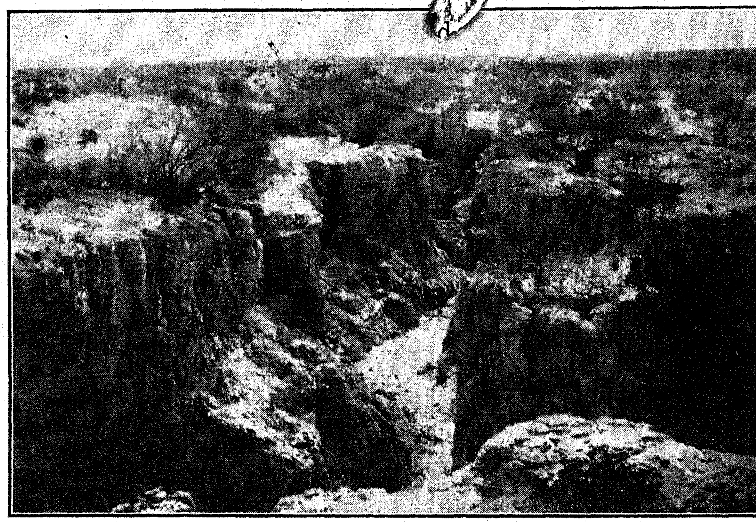

Fig. 53.—Erosion and deposit in a young ravine in the bad lands of Nebraska.

Gravity produces bare areas by pulling down materials freed by weathering (Fig. 54). Crumbling and slipping are universal processes on the steep slopes of crests and hills and along stream banks and lake- and

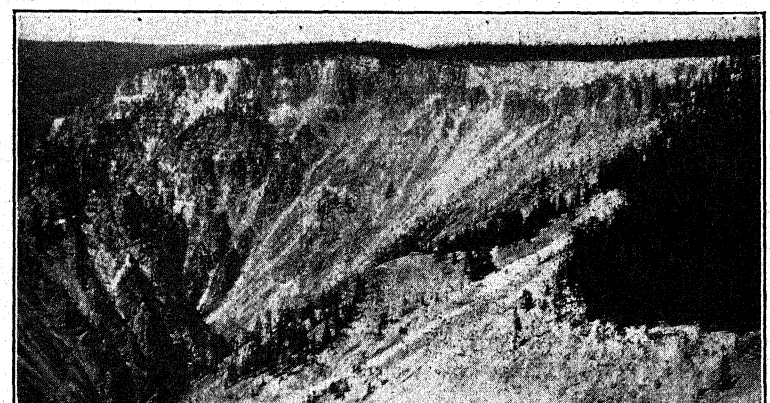

Fig. 54.—Bare areas due to the action of gravity, cañon of the Yellowstone River, Yellowstone National Park.

seashores everywhere. Landslides in mountains as well as heavy snow-slides often produce extensive bare areas. From their hardness, instability, or dryness and the steep or vertical faces, areas thus produced are usually among the slowest to be invaded.

Bare areas are produced on wind-swept shores by the grinding and pushing action of ice. Fine illustrations are to be found in the region of the Great Lakes. Bare areas are also formed along the margins of glaciers, usually in conjunction with water erosion. The extreme conditions which rock invaders must meet in the Rocky Mountains and Sierra Nevada are often the direct outcome of glacial scourings in the past.

Bare Areas Due to Deposit.—Bare areas are often due to deposit, the agents being running water, ground water, wind, glaciers, ice and snow, gravity, and volcanoes.

FIG. 55.—Sand bars due to deposit in streams. North Platte River in Nebraska.

Among bare areas due to deposit by running water, flood plains and channel deposits such as sand bars and alluvial cones and fans are perhaps most familiar (Fig. 55). Other deposits such as deltas and beds of lakes are often extensive. Along the shores of large bodies of water, waves and tides produce such bare areas as beaches, reefs, bars, and spits.

Characteristic deposits from ground water are made by mineral springs, especially hot springs, and geysers. Travertine or tufa is formed from water highly charged with lime and is deposited in lakes of dry regions as well as from spring waters and their streams. Siliceous sinter or geyserite is typical of the areas about geysers where it arises by deposition from the hot siliceous waters, through the action of algæ. Both travertine and sinter are rock and exhibit the general relation of rocks to succession, the first colonists being algæ and lichens. Salt may be deposited from spring waters, as in salt basins, or by the water of lakes in arid regions where evaporation exceeds the inflow. In moist and semiarid regions, the salt crust is usually thin and, hence, readily dissolved or weathered away, permitting halophytes to enter and begin

the succession. In arid regions, on the contrary, the deposits are thicker, and removal by weathering or solution is nearly impossible, so that extensive areas, in Utah and Nevada for example, remain absolutely sterile under present conditions.

The principal wind deposits are sand, chiefly in the form of dunes, loess, and volcanic dust. Of these, dunes, both inland and coastal, are much the most important at the present time (Fig. 56). The wide distribution of dunes and their striking mobility have made them favorite subjects of investigation and there is probably no other initial area and succession of which we know so much. Inland dunes of the Great

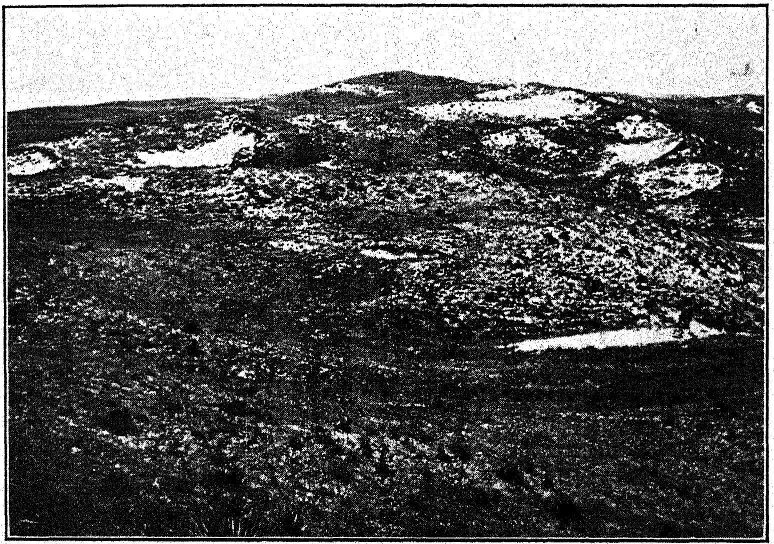

Fig. 56.—Sandhills showing blow-outs.

Plains are called sandhills. In spite of the irregularity of the topography of dunes, they affect succession by virtue of instability and water relations and not by form. Sandhills, deep hollows or blow-outs, and sandy plains all show the same development, regardless of their difference in form. In all of these the controlling part is played by the sand-catching and sand-binding plants, usually grasses, which act as pioneers. The chief reactions are the fixation of the sand, gradual accumulation of humus, and decrease of evaporation and increase of water content. Loess, while covering enormous areas in the valleys of the Mississippi, Rhine, Danube, Hoang-Ho, and other rivers, is not in process of formation today. Deposits of volcanic dust are infrequent and localized and cover relatively small areas. They are unique in the suddenness and completeness with which the area is covered and in their absolute sterility.

Glaciers, ice, and snow are agents that often cause extensive deposits. Glaciers have been of the greatest importance in the past, although today their action is localized in the mountains and polar regions as is also that of snow and ice. They deposit materials showing all possible degrees of variation. The enormous blocks of rocks deposited by glaciers present an extreme condition for rock succession; the till sheet proper of clay mixed with sand and pebbles offers an area prepared for a higher type of colonists. All intermediate conditions occur.

Bare areas due to deposit by gravity such as talus masses and slopes are universal at the base of cliffs, shores, banks, etc. The initial conditions for succession are often very like those of the cliff or bank above. The chief change is one of density or coherence. Hence, the lichens or cleft plants of a granite cliff or wall are usually found in the talus as well, even when this is disintegrated to the stage of coarse gravel. Talus derived from soils such as sand or clay or from rocks which decompose readily presents typically more extreme conditions as to water content and stability than the fragmenting area. Here the initial stages are new and unlike those at the top of the cliff or bank. Whether they will be hydric or xeric is determined by the location of the talus and its resulting water content.

Volcanoes produce bare areas by deposits of lava, of cinders so called, of ash or dust, and of sinter. The deposits of ash may be local, sometimes reaching depths of 50 to more than 100 feet, or scattered widely by the wind; coarser materials—cinders, rocks, and enormous stones—are also blown from craters in great quantities and fall near the cone or upon its slopes. The lava and mud expelled from volcanoes flow in streams from the crater. Rivers of lava have been known to reach a length of 50 miles and a width of ½ mile. In flat places, the stream spreads out and forms a lava lake which hardens into a plain. Mud volcanoes are small, geyser-like structures which discharge mud. They build up small cones, which are usually grouped and cover considerable areas. The deposits due to volcanoes or geysers regularly result in the destruction of vegetation, but this effect may be produced in consequence of the emission of poisonous gases, steam, hot water, hot mud, or fire blasts or the heating of the soil. Such bare areas are characteristic features of Yellowstone National Park.

All volcanic deposits are characterized by great sterility.[197] They are usually small in extent and, hence, easily accessible to migrants. The seres on volcanic deposits have been little studied, but it is known that they are relatively long. This is particularly true of lava, though climate exerts a decisive effect, as is shown by the invasion of lava fields in Iceland[373] and Java.[156]

Other physiographic causes of bare areas are earthquakes and possibly also the rapid elevation or subsidence of the land.[90]

Climatic Causes.—Climate may produce new areas for succession through the destruction of existing vegetation. This destruction may be complete or partial. When it is complete or nearly so, a bare area with more extreme water conditions is the result. The factors which act in this manner are drought, wind, snow, hail, frost, and lightning. In addition, evaporation, which is the essential process in drought, produces new areas from water bodies in semiarid and arid regions. It may have the same effect upon periodic ponds in humid regions. Evaporation may merely reduce the water level to a point where ecesis of hydrophytes is possible, or it may continue to a point where islands, peninsulas, or wide strips of shore are laid bare to invasion. Finally, the lake or

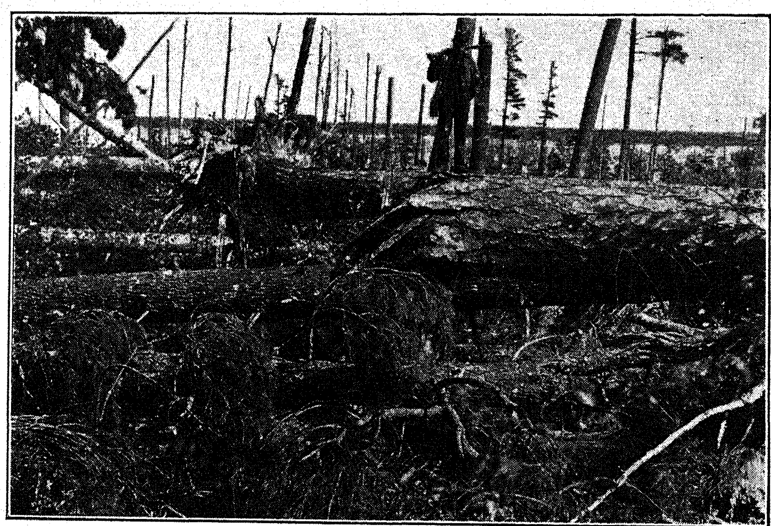

FIG. 57.—Wind-throw in a pine forest in Minnesota.

pond may disappear entirely, leaving a marsh, a moist or dry plain, or a salt crust.

The action of drought in destroying vegetation and producing areas for colonization is largely confined to semiarid and arid regions. In humid regions it is neither frequent nor critical, while in desert regions it is the climax condition to which vegetation has adapted itself fully or nearly so. The usual effect is to produce a change in existing vegetation, but in regions like the Great Plains it sometimes destroys vegetation completely. As a rule, the destruction operates upon cultivated fields, simply freeing the area somewhat earlier for the development of a ruderal or weed stage. It also occurs in tree plantations with somewhat similar results. In native vegetation the complete destruction of a community is rare.

The wind acts directly upon vegetation in producing bare areas due to "wind-throws" (Fig. 57). Areas where trees have been blown down by the wind are frequent in some regions but usually are of limited extent. They are most apt to occur in pure stands of such trees as balsam fir, spruce, and lodgepole pine. "Wind-throws" are frequent in mountainous regions where the soil is moist and shallow. The action of the wind chiefly affects the tree layer and tears up the soil as a consequence of uprooting the trees. It is supplemented by evaporation, which destroys the shade species by greatly augmenting their transpiration

FIG. 58.—An old "burn" in eastern Washington. Typical of the destruction by fire of coniferous forests of the Northwest. (*Photo by Palmer.*)

at a time when the water content is being diminished by the drying of the soil. As a consequence, "wind-throws" often become completely denuded of vegetation. In the case of a completely closed forest, the fall of the trees amounts to denudation, since occasional saprophytes are often the only flowering plants left.

Bare areas may be due to snow, hail, or frost. Those due to snow are restricted largely to polar and alpine regions. An abnormal fall or unusual drifting may cause the snow to remain in places regularly exposed each summer. After a winter of less precipitation or a summer of unusual heat, the drifts or fields will melt, leaving a bare area for invasion. The effect of frost in producing bare areas by destroying the plant population is almost negligible but the denuding action of hail is often very great. In some parts of the Great Plains, destructive

hailstorms are so frequent that they have caused the abandonment of farms and sometimes whole districts. It is not infrequent to see the fields so razed by hail that not a single plant is left alive. Native species often suffer great damage, especially broad-leaved forest and scrub, but the effect rarely approaches denudation. As with frost, the effect upon cultivated plants is very much greater than upon native vegetation.

The rôle of lightning in causing fire in vegetation has come to be recognized as very important. The majority of lightning strokes do not set fire to trees or other plants and the attendant rain usually stops incipient burns. Even under these conditions, forest fires have actually been seen to start from lightning and the number of such cases in the aggregate would apparently be large. In regions where thunderstorms unaccompanied by rain are frequent, as in Montana and Idaho, lightning is the cause of numerous, often very destructive, fires (Fig. 58).

Bare areas may result indirectly from climatic factors. These are due almost wholly to the effect of physiography in exceptional cases of rainfall, of run-off due to melting snow, or of wind-driven waters. In all three the process is essentially the same. The normal drainage of the area is overtaxed. The flood waters reach higher levels than usual and are ponded back into depressions rarely reached. Moreover, they cover the lowlands for a much longer period. In the one case, they form new water areas for invasion. Since these are usually shallow and subject to evaporation, the development in them is nearly always a short one. In the case of lowlands, the vegetation of many areas is washed away, covered with silt, or killed by the water, and the area is bared for a new development. This is, of course, essentially what must have occurred at the end of each period of glaciation.

Biotic Causes.—With few exceptions, plants rarely play the rôle of initial causes. The reactions of plant communities on the habitat are of paramount importance but plants rarely destroy vegetation and produce bare areas. The reverse is true of man and animals. They are initial causes of great frequence and widespread distribution, but only a few have a definite reaction upon the habitat. Their activities may be grouped as follows: (1) activities which destroy vegetation without greatly disturbing the soil or changing the water content; (2) activities which produce a dry or drier habitat usually with much disturbance of the soil; and (3) activities which produce a wet or wetter soil or a water area.

Bare areas are sometimes due to destruction of vegetation alone. Ant areas in arid regions are, perhaps, the best examples of clearing by animals without soil disturbance (Fig. 59). The primary activities by which man produces denuded areas are burns and clearings. Clearings result, for the most part, from lumbering or from cultivation. In all cases of burning and clearing, the intensity or thoroughness of the process

determines whether the result will be a change of vegetation or the initiation of a new sere. The latter occurs only when the destruction of the vegetation is complete or so nearly complete that the pioneers dominate the area. Lumbering consequently may not initiate succession unless it is followed by fire or other process which removes the tree seedlings and destroys the undergrowth. Most fires in woodlands completely denude the burned area, but surface fires and top fires may merely destroy a part of the population. Fires in grassland practically never produce bare areas for colonization. Poisonous gases from smelters, factories, etc., sometimes result in complete denudation, although the effect is

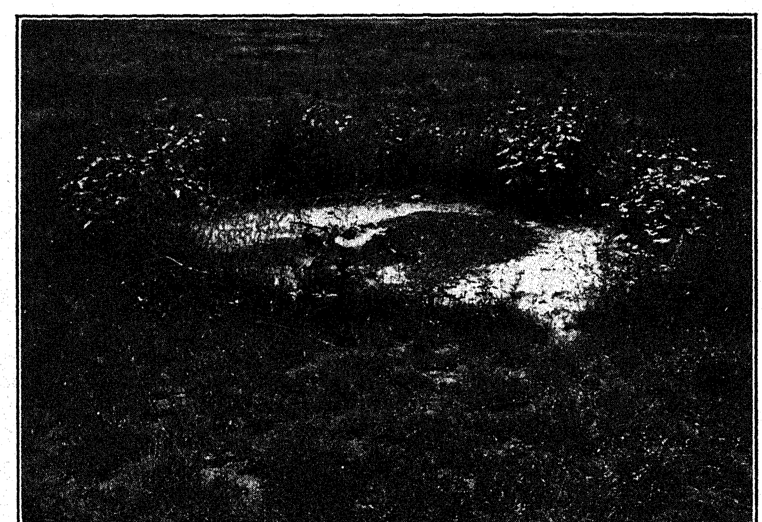

FIG. 59.—Bare area 3 to 4 feet in diameter due to ants. Note the invasion of sunflowers, etc., about the periphery of the bared area and the better growth of the vegetation resulting from an increased water supply.

usually seen in changes in the vegetation. Cultivation normally results in complete destruction of the original vegetation. In new or sparsely settled grassland regions, the wearing of roads or trails produces a characteristic denudation with little or no soil disturbance.[463] Complete denudation by animals is only of the rarest occurrence, except where they are restricted to limited areas by man. Severe overgrazing and trampling by stock are examples. Complete destruction by parasites usually occurs only in the case of annual crops.

Bare areas may result from a dry or drier soil. These occur chiefly where there is a marked disturbance of the soil. The latter affects the water content by changing the structure, by changing the kind of soil, as from clay to sand or gravel, or by both methods. These results may be produced by removal, by deposit, or by the stirring of the soil in place. Roads and railroads are universal examples. In surface or "strip"

mining for coal or iron, enormous areas are laid bare, the raw subsoil brought to the surface, and sometimes, also, materials which upon oxidation produce extreme acidity.[131] Gravel pits and deposits formed by dredging and draining are other examples. The removal and deposit of soil by animals are confined to the immediate neighborhood of their burrows, the homes of ants, etc. In some cases, such as densely populated prairie-dog towns, the burrows are sufficiently close to produce an almost completely denuded area. Insignificant as most areas of this sort are, they give rise to real though minute seres of much value for successional studies in communities otherwise little disturbed.

Bare areas may occur as a result of increase in water. Draining and flooding may bring two different areas (*e.g.* a pond and a valley) to the same condition for invasion. The habitats produced by both are similar in having a wet soil, capable of colonization only by hydrophytes, except in cases where drainage is reinforced by rapid or excessive evaporation. This is true of canals and ditches as well as of the areas actually drained or flooded. It is unimportant whether flooding, for example, is brought about by the diversion of a stream of water or the construction of a dam. It is equally immaterial whether the dam is built by man or by beavers. The essential fact is that the water content will be excessive and that the pioneers will consist of hydrophytes in all these cases.

To Study the Initial Causes of Succession.—In the course of the field work, give careful attention to the kinds of bare areas in your region and the causes for their production. Make a list of all of the bare areas you have seen. What cause or causes operate most widely in producing bare areas in the regions that you have studied?

CHAPTER VI

AGGREGATION, MIGRATION, AND ECESIS

It has been seen how the field of action for the development of plant communities has been prepared by the various initial causes. But it seems clear that, regardless of the kind or extent of the bare area, succession will not occur unless other causes are at work. The real causes of the development of vegetation, *i.e.* the paramount causes of succession, are the responses or adjustments that the successive communities make to the habitat. These are aggregation, migration, ecesis, competition, and reaction. To them is due the rhythm of succession as expressed in the rise and fall of successive populations.

AGGREGATION

All sterile, bare areas owe their pioneers to migration. But after the establishment of the first invaders, the development of families and colonies is due primarily to aggregation, the process by which germules come to be grouped together. It consists really of two processes, simple aggregation, *e.g.* the grouping of germules about the parent plant, and migration. This coming together of individual plants is the process that produces vegetation. It gives rise to the innumerable groups of varying rank which taken together make up vegetation.

In its simplest form, aggregation is the immediate result of reproduction, but, as a rule, the movement or migration of the individuals plays an equally important part. The simplest cases of aggregation are where the germules are grouped about the parent plant. It is independent of migration. Although in the falling of seeds there is often some movement away from the parent plant, it can not properly be regarded as migration unless the seed is carried into a different family or into a different portion of the same colony. The distinction is not always a sharp one but rests on two factors of much importance. The first is that movements within the family bear a different relation to ecesis than movements beyond the parent area. Secondly, simple aggregation increases the individuals of a species and tends to produce its dominance, while migration has just the opposite effect. Aggregation at once gives rise to competition between the aggregated individuals, and upon the outcome of this depends their adjustment or establishment. In the majority of cases, simple aggregation is prevented by the migration of

the seeds or fruits away from the parent plants. But here, again, the final grouping of the individuals depends upon ecesis and competition.

Simple Aggregation.—The simplest examples of this process occur in such algæ as *Glœocapsa* and *Tetraspora,* in which the plants resulting from fission are held together by a sheath of mucilaginous materials. The relation of the plants is essentially that of parent and offspring, even when the parent disappears regularly, as in the fission algæ, or sooner or later, as in the case of annuals. Practically the same family grouping occurs in the case of terrestrial forms, flowering plants especially, where the seeds of a plant mature and fall to the ground about it

FIG. 60.—Simple aggregation of the seedlings of bug-seed (*Corispermum*) about the parent plant.

(Fig. 60). The size and density of the family group are determined by the manner of reproduction and especially by the number of seeds produced. The character of the family is also affected by the height and branching of the plant and the position of the seeds upon it. The family will be small and definite in case of species whose fruits or seeds are immobile, *i.e.* not well adapted for migration, the seeds falling directly beneath the plant (*e.g.* sunflowers, ragweeds). A similar group is often produced by offshoots (*e.g.* false Solomon's-seal, nettle) when they do not carry the new plants too far from the original one.

If the fruits or seeds are mobile, the degree of aggregation in the family is correspondingly decreased, since the seeds are carried away from the parent. Very mobile forms such as the dandelion rarely produce families for this reason, and this is often true also of plants

which produce few seeds. Annuals occur more frequently in families, owing to the large number of seeds and the frequent absence of devices for migration. Many perennials also arrange themselves in families, especially those that are immobile or migrate by means of underground parts.

These facts illustrate the law of simple aggregation, *viz.* that lack of dissemination promotes the grouping of parent and offspring into families, while mobility hinders it. Families are produced more readily in new and denuded habitats, *i.e.* in open communities than in closed ones, since in the latter individuals of various species have already become mingled with each other. If all species were immobile, families would to a large degree be characteristic of vegetation. Since the great majority are more or less mobile, groups of this sort are the exception rather than the rule.

Aggregation usually modifies the composition and structure of existing communities. Its influence is especially important in communities destroyed by fire, cultivation, etc. In many instances, the change in soil conditions is slight and the course of succession is determined by the number of germules which survive. In forests, for example, if the number is large, the resulting sere is very short, consisting only of the stages (usually herbaceous and shrubby) which can develop while the trees are growing to the size which makes them dominant. But when the number of aggregated germules is small or none, the selective action of migration comes into play—the climax must await the arrival of the dominants—and the course of development is correspondingly long.

Mixed Aggregation.—Individuals are carried away from the family group by migration, and strange individuals are brought into it by the same means (Fig. 61). In the early growth of a family, due to the gradual spreading of the plants, neighboring families approach each other and finally mingle more or less completely. In both cases, the mixing of the two or more species to form a colony is due to migration. The conversion of a family into another community takes place usually through the invasion of mobile species. The change occurs when one or more individuals of a second species becomes established in the family group. The real nature of the community becomes more evident when several generations have brought about a considerable increase in numbers.

The appearance of each successive stage in succession is brought about by the interaction of migration and aggregation. Migration brings in the species of each stage and aggregation causes them to become characteristic or dominant. Migration marks the beginning of the initial, medial, and ultimate stages of a sere. It becomes relatively more marked with successive stages (*i.e.* more kinds of plants are found in

medial stages) and then falls off to a minimum. In dense, closed forests, it becomes extremely rare, and the ecesis of the migrants impossible. Aggregation, on the other hand, becomes more marked with successive stages, and a sere may end in what is essentially a family, *e.g.* a pure stand of Douglas fir or Engelmann spruce with practically no undergrowth.

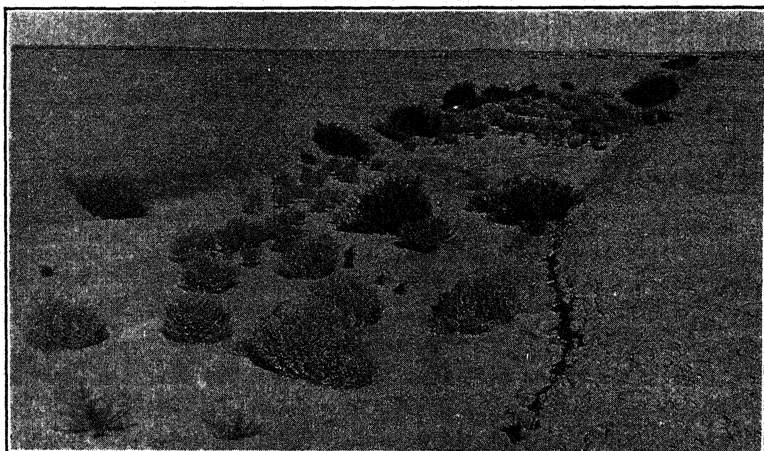

FIG. 61.—A colony of sea blite (*Dondia*) and orach (*Atriplex*) in a depression, showing mixed aggregation.

MIGRATION

Migration begins when the germule leaves the parent area and ends only when it reaches its final resting place. It may consist of a single movement, or the number of movements between the two places may be many, as in the repeated flights of fruits with wings or pappus. The entrance of a species into a new area or region will often result from repeated invasions, each consisting of a single period of migration and ecesis. This is well illustrated by the invasion of the Russian thistle (*Salsola pestifer*). It was introduced into South Dakota in 1874 with imported flax seed. By 1888, there were enough plants in the Dakotas to have it reported as a weed. Ten years later, it was found in all the area east of the Rocky Mountains, from the Gulf of Mexico to Saskatchewan.[190] Evidence of past migration is shown by the fact that where suitable places for particular groups of plants occur (*e.g.* swamps, rock outcrops, etc.), they are nearly always found growing there.[506] Germules of various kinds find their way into communities but only a very few find suitable habitats not already overcrowded in which they can ecize. It is only by the process of migration that the plants of any stage in a sere are brought into the new area.

To Determine What Propagules Have Migrated into a Bare Area.—Select a bare area such as a flood plain, talus slope, or fallow field. Remove enough of the surface

soil from an area of 2 square decimeters to fill a 4-inch flowerpot. Place under favorable conditions for growth. When the seedlings of the first crop have been counted and identified, remove them. Pour out the soil, mix it thoroughly in order to permit dormant seeds to germinate, and grow another crop. Repeat the process until no more seedlings appear. Record the total number of species and individuals.

The four factors entering into migration are *mobility*, *i.e.* the ability of a species to move out of the parent area, *agent* (wind, water, etc.), *distance*, and *topography*. These are not always present in every case of migration, but, as a rule, each factor plays some part. The value of mobility to the plant is dependent upon the presence of proper agents for causing movement, and the operation of these two factors is much affected by distance and topography.

Mobility.—Mobility indicates the power of the plant for movement. Among terrestrial plants it is indicated chiefly by the size, weight, and surface of the disseminules, especially those carried by wind and water. A small, light seed or fruit with a wing, such as elm or birch, is much more mobile than a large, heavy, smooth one, such as the walnut. Man and animals distribute fruits for so many reasons and in so many ways that the only test of mobility, in many cases, is the actual movement. This is especially clear in the case of many weeds of cultivated fields which owe their migration wholly to their associates, *i.e.* cultivated crops. Although mobility depends primarily upon devices for bringing about dissemination (hooks, plumes, etc.) the number of seeds is also an important factor. It is increased by large seed production, first because among the larger number of seeds or fruits some may get out of the parent area, and, secondly, because of their correspondingly smaller size.

Mobility is most marked in those plants which are themselves mobile such as bacteria, diatoms, volvox, etc., or possess motile spores as among some of the green algæ. On the other hand, it is little or not at all developed in flowering plants with large, heavy seeds or fruits. The range is extreme, from the almost immobile offshoots of lilies, which move by growth, to the non-motile but very mobile spores of fungi, which are blown about by the wind. There is no necessary correspondence between mobility and motility. The latter is practically absent in terrestrial plants, and, in spite of its importance among the algæ, it plays a relatively small part in migration.

Mobility depends not only on the nature of the device for dissemination and upon the number of germules produced but also is greatly influenced by the position of seed or spore with reference to the action of the distributive agent. Winged fruits, for example, are nearly confined to trees or shrubs or high-climbing vines. They would be much less mobile if borne near the soil.

The relation of mobility to succession is obvious. Fireweeds, among the earliest pioneers in bare land areas, and especially in denuded ones, have

very mobile germules. The spores, soredia, and gemmæ of lichens, liverworts, and mosses are microscopic in size and broadly disseminated by wind. The early herbaceous pioneers are grasses and herbs with small seeds and fruits, well adapted for wind carriage, as in fire grass (*Agrostis*

FIG. 62.—Fireweed (*Chamænerion*) in a burned area in Idaho.

FIG. 63.—Pioneer willows and cottonwoods on a sand bar in the Missouri River. If the bar is built up these will be replaced by elms, linden, etc.

hiemalis) and fireweed (*Chamænerion angustifolium*), or mobile by virtue of association (*i.e.* moved by man with his crops) as the mustards (*Brassica* and *Lepidium*) and goosefoot (*Chenopodium*) (Fig. 62). The sequence of shrubby species is determined partly by mobility, as berry-producing

shrubs in burns (*Rubus*), and willows (*Salix*) in lowlands (Fig. 63). Likewise, cottonwoods (*Populus*) and birches (*Betula*), which have light, wind-blown seeds, are everywhere woodland pioneers. Rapid occupation of a new area depends upon mobility, but in permanent occupation it is much less important. Fireweed may soon occupy a burned forest area, but it does not occur in the reestablished climax.

Organs of Dissemination.—Plants differ much with respect to the organ modified or utilized for dissemination. Such modification, while it usually affects the fruit or seed alone, may act upon any organ or upon

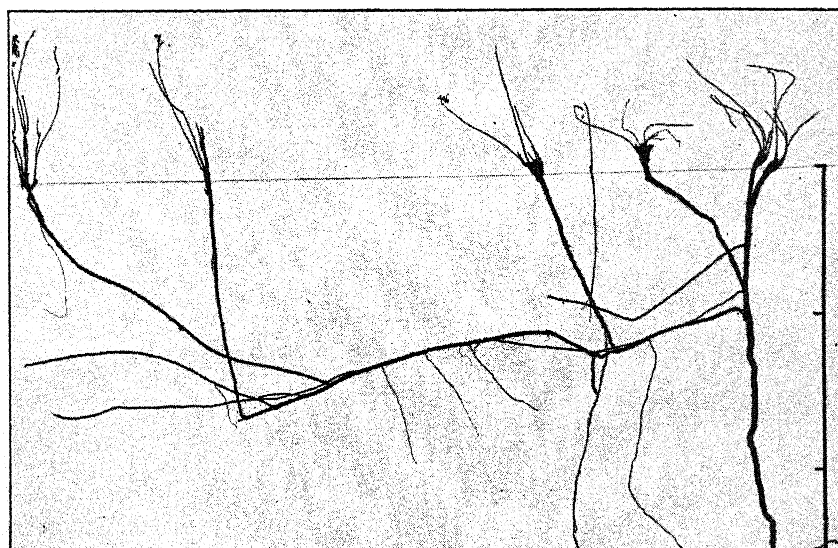

FIG. 64.—A wild rose (*Rosa arkansana*) showing the method of propagation by underground offshoots. Scale in feet.

the entire plant body. Special modifications are usually developed in connection with spores and seeds, and mobility is most marked in species of this sort. It is much reduced in the case of offshoots such as rhizomes, stolons, and root sprouts and in plant bodies, at least in terrestrial plants, notwithstanding a few striking exceptions, such as the tumbleweeds. Plants may be grouped as follows with reference to the part distributed:

Spore Distributed.—This group includes all plants possessing structures which are called spores, *viz.* algæ, fungi, liverworts, mosses, and ferns. Spores rarely have special devices for dissemination but their minute size makes them extremely mobile. In general, spores are more readily and widely distributed than are seeds or fruits. They are blown about like the dust. Tropical islands, for example, are notable for their fern population.

Seed Distributed.—This group comprises all flowering plants in which the seed is the part modified or disseminated. Seeds are not very mobile except when they are minute or are provided with wings or hairs. They are, however, as a group more mobile and more widely distributed than fruits, largely because of their smaller size.

Fruit Distributed.—The modifications of the fruit for distribution exceed in number and variety all other modifications for this purpose. Many structures which are commonly mistaken for seeds belong here. Such are the achene (of sunflowers, and other composites, etc.), caryopsis (of wheat and other grasses), perigynium (of sedges), and utricle (of chenopods and amaranths), etc.

Offshoot Distributed.—To this group are referred all plants that produce lateral shoots, such as root sprouts, rhizomes, stolons, etc. When new buds are thus carried from several to many feet from the parent plant, *i.e.* out of the area under parental influence, the results may well be regarded as migration rather than aggregation. The migration of such plants is very slow, but it is usually effective, since the new plant is nourished by the parent until it becomes fully established (Fig. 64). It plays a small part in the colonization of new areas, being almost negligible in comparison with the migration of free parts such as spores, seeds, and fruits, especially in large areas.

Plant Distributed.—This group includes submerged and surface water plants, both motile and non-motile, and those land forms in which the whole plant, or at least the aerial part, is distributed, as in tumbleweeds and many grasses.

Modifications for Migration.—Plants may be arranged in the following groups according to the nature of the device by which migration is brought about. The perfection of the device determines the success of the agent, as is well seen in those modifications which increase the surface for wind carriage.

Saccate.—The species of this group possess various fruits all of which agree in having sac-like envelopes. These may be membranous and serve for wind distribution, as in ironwood (*Ostrya*), ground cherry (*Physalis*), and bladder nut (*Staphylea*), or impervious and air containing, as in sedges (*Carex*), water lily (*Nymphœa*), etc., where they serve for water transport. Sack and bladder fruits, as in ground cherry, are relatively ineffective and are often associated with other devices such as fleshiness (Fig. 65).

Winged.—This group includes all winged, margined, or flattened fruits and seeds, such as are found in maple (*Acer*), birch (*Betula*), dock (*Rumex*), and many members of the carrot and grass families. Wings often contain air spaces of considerable size and give greater buoyancy than the preceding but are only moderately efficient except where the seed is small and light. The vast majority of the samaras of elm, maple

ash, etc., fall near the parent tree. This is usually also true of the seeds of conifers (Fig. 66). A careful transect study of the flight of seeds of the spruce and the fir showed that practically all of them landed

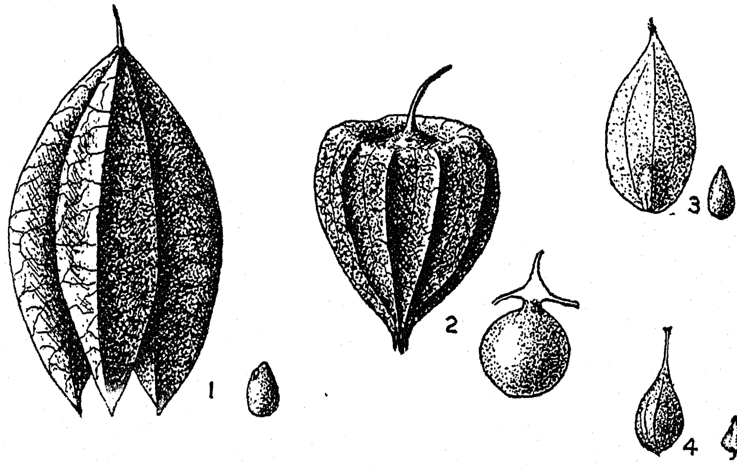

FIG. 65.—Sac-like envelopes with (1) seed of bladdernut (*Staphylea*), (2) fruit of ground cherry (*Physalis*), (3) seed of ironwood (*Ostrya*), and (4) achene of *Carex*, about natural size except *Carex* which is × 1.5.

within a distance equal to two or three times the height of the tree. Where isolated seed trees are left standing, as in lumbering operations, the distance to which the seeds may be carried is greatly increased.[241]

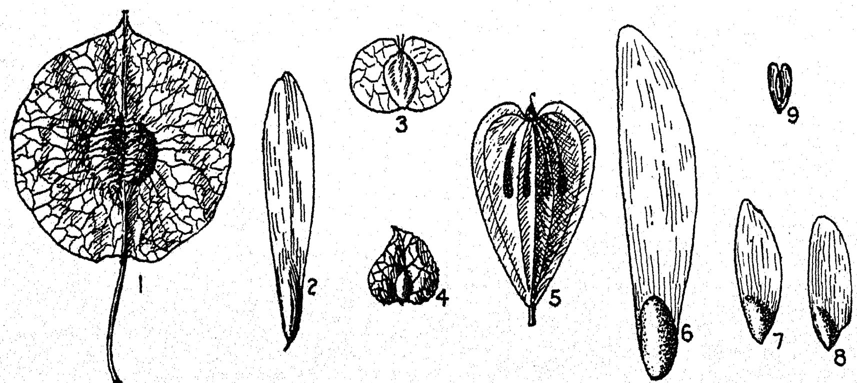

FIG. 66.—Winged seeds or fruits of (1) hop tree (*Ptelea*), (2) ash (*Fraxinus*), (3) birch (*Betula*), (4) dock (*Rumex*), (5) cow parsnip (*Heracleum*), (6) western yellow pine (*Pinus*), (7) Douglas fir (*Pseudotsuga*), (8) western hemlock (*Tsuga*), and (9) white cedar (*Thuja*), all about natural size except 3, 4, and 5 which are × 2.

Comate.—To this group belong those fruits and seeds with long, silky hairs such as windflowers (*Anemone*), milkweed (*Asclepias*), cotton (*Gossypium*), cottonwood (*Populus*), etc., and those with straight capil-

lary hairs or bristles not confined to one end, willow (*Salix*), cattail (*Typha*), etc. (Fig. 67).

Parachute.—These are the parachute-like achenes of the dandelion (*Taraxacum*), lettuce (*Lactuca*), and other ligulate composites. Through the cotton grass (*Eriophorum*) and others, this group is connected with the preceding one (Fig. 68). Parachute fruits represent the highest

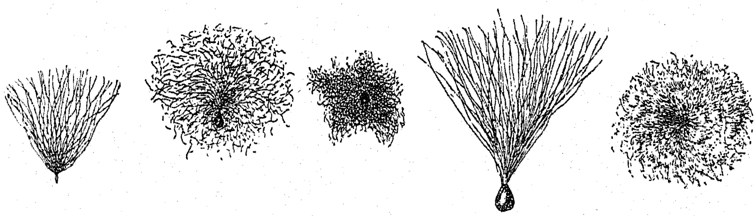

FIG. 67.—Comate seeds of fireweed (*Chamænerion*), cottonwood (*Populus*), achene of windflower (*Anemone*), and seeds of milkweed (*Asclepias*) and cotton (*Gossypium*), about natural size except last two which are × ½.

degree of mobility that has been obtained by special modification. Comate and parachute seeds and fruits are by far the most efficient of wind-blown disseminules and probably of all kinds, as well. Success is determined largely by smallness of size, but apart from this the perfection of the device as to the number, length, and position of scales or hairs is decisive. Disseminules tufted at one end are carried more readily than

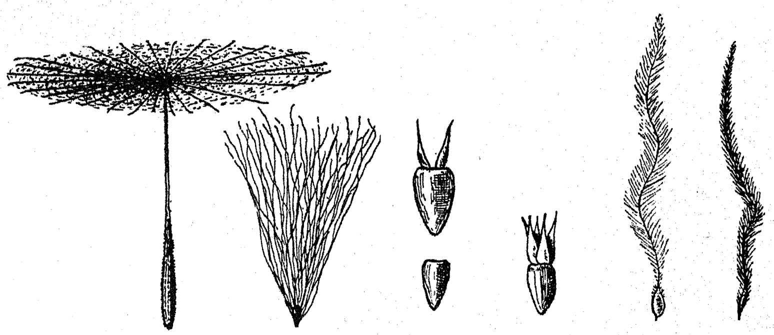

FIG. 68.—Parachute and achene of salsify (*Tragopogon*), bristly achene of cotton grass (*Eriophorum*), chaffy achene and seed of sunflower (*Helianthus*), chaffy achene of *Marshallia*, and plumed achenes of *Clematis* and pasque flower (*Pulsatilla*), all about natural size.

those covered with hairs, but a pappus which spreads widely or is plumose is the most effective of all.

Chaffy.—In this group are placed those achenes with a more or less scaly or chaffy pappus which gives slight mobility, as in niggerheads (*Brauneria*) and sunflower (*Helianthus*), etc. Scales are less efficient than bristles or hairs, but the latter are successful in proportion to their length and number (Fig. 68).

Plumed.—In fruits of this kind, the style is the part usually modified into a long, plume-like organ, producing a high degree of mobility, as in clematis and pasque flower (*Pulsatilla*).

Awned.—These are nearly all grasses in which the awns serve for distribution by water or animals and even by creeping movements.

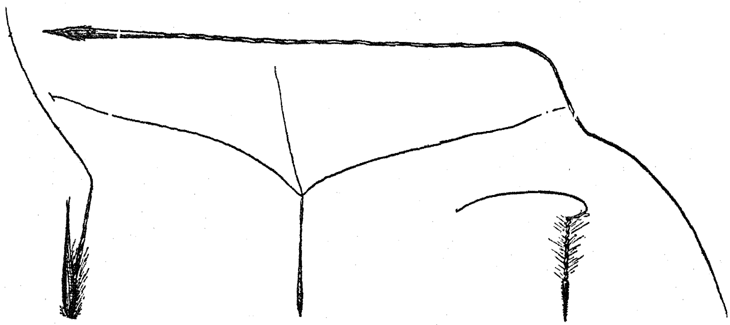

FIG. 69.—Awned seeds of wild oats (*Avena*), three-awned grass (*Aristida*), stork's-bill (*Erodium*) and (above) needle grass (*Stipa*), about three-fourths natural size.

The degree of mobility, in many cases, is great. Needle grasses (*Stipa*), three-awned grasses (*Aristida*), wild oats (*Avena*), and the stork's-bill (*Erodium*) belong here (Fig. 69).

Spiny.—This group contains a few species in which distribution of the spiny fruits is brought about by attachment, as sand bur (*Cenchrus*) and ground bur nut (*Tribulus*) (Fig. 70).

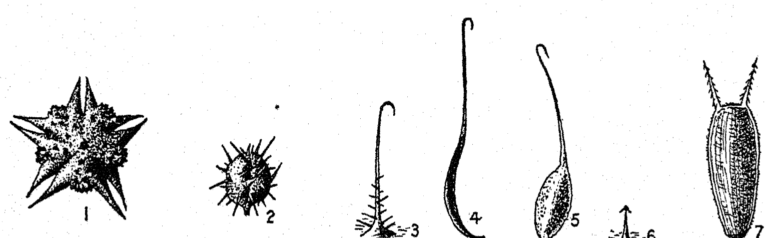

FIG. 70.—Dispersal by spines and hooks. (1) ground bur-nut (*Tribulus*), (2) sand bur (*Cenchrus*), (3) cocklebur (*Xanthium*), (4) burdock (*Arctium*), (5) white avens (*Geum*), (6) stickseed (*Lappula*), and (7) beggar-ticks (*Bidens*). 1 and 2 are natural size, 7 is twice, and the rest three times natural size.

Hooked.—The members of this group are extremely numerous, and the degree of mobility is, as a rule, very high. All agree in the possession of hooks and barbs which serve for attachment, though the number, size, and position of the hooks vary greatly. Here belong the cocklebur (*Xanthium*), burdock (*Arctium*), beggar-ticks (*Bidens*), white avens (*Geum*), stickseed (*Lappula*), etc. The number of pioneers which possess fruits with spines or hooks is significant.

Viscid.—In these the inflorescence is more or less covered with a viscid substance, as in species of pinks (*Silene*), or the fruit is beset with sticky hairs, as in chickweed (*Cerastium*), certain sages (*Salvia*), and twinflower (*Linnæa*).

Fleshy.—These are fleshy fruits which are scattered in consequence of being swallowed, especially by birds. The seeds are usually protected by a stony envelope which enables them to resist digestion. Many fruits are carried some distance where the seed is discarded after the fleshy portion has been eaten. The mobility varies greatly, but the area over which migration may be affected is relatively large.

Flagellate.—These are plants with cilia or flagellate spores, as in certain algæ such as *Œdogonium*, *Ulothrix*, *Vaucheria*, or with plant bodies similarly motile, bacteria, volvox, and others.

Migration.—In the fall of the year, make a careful survey of a bare area that is being populated and classify the plants (1) as to the organ utilized in migrating into the area and (2) the nature of the device by which migration was brought about. Identify and classify 50 or more propagules of plants common to your region upon the basis of modifications for migration. The relative efficiency of some of the various migrating devices should be determined as on page 30.

Distance of Migration.—The distance of migration is a direct consequence of the perfection of the device. Hence, the latter is of first importance in selecting the migrants which are moving toward a new area. It thus plays a large part in determining what species will enter as pioneers as well as the stages in which others will appear. The comate seeds of fireweed, aspen, and willow may be carried several miles in such quantities as to produce dominance. In secondary areas especially, dominance is directly dependent upon the number of viable seeds which enter and, hence, upon the migration device. If seeds or one-seeded fruits migrate singly (*e.g.* maple, elm), the resulting individuals stand separately. Dominance results only from the movement of large numbers. Where germules travel in groups, as tumbleweeds (*Salsola*, *Cycloloma*) or cockleburs adhering in mats, the new area is at once dominated by families.

Interaction and Work of Agents.—Many fruits migrate readily even when the devices for migration are not greatly perfected. This is due to the fact that they avail themselves of two or more agents, either by means of two distinct devices or because of their behavior on drying. In the ground cherry, the bladdery fruit is rolled over the ground by the wind and then the seeds are scattered by birds and rodents. *Pilobolus*, a dung-inhabiting fungus, discharges its mucilaginous masses of spores upon adjacent weeds and grasses, where they can not grow. But when the vegetation is eaten by animals, the spores pass unharmed through the alimentary tract and are deposited in a suitable substratum for germination and growth. Needle grass, stork's-bill, and other plants

with sharp-pointed, twisting fruits are carried by attachment to animals and blown by the wind in tangled clusters, the two agents often alternating many times. The wild balsam apple (*Micrampelis*) is a frequent pioneer in denuded areas along streams. The fruits are blown by the wind, floated by streams, and even carried by attachment, while the seeds, in addition to being forcibly expelled, are carried by water.

Although the possibilities of the interaction of two or more agents in nature are great, actual instances of it are not frequent except where the activities of man enter into the question. Seeds and fruits are frequently blown by the wind into streams by which they are carried away. As a rule, however, parts adapted to wind distribution are injured by immersion in the water, and the number of plants capable of being scattered by the successive action of wind and water is small. As a general rule, plants growing in or near the water, if modified for migration at all, are adapted to water carriage. Species that grow in exposed grassy or barren habitats are, for the most part, wind carried. Those found in the shelter of forests and thickets are usually scattered by animals, though the taller trees and shrubs are generally wind distributed by reason of exposure to the upper air currents. There is seen to be a certain amount of correspondence, since hydrophytes are usually water carried, shade plants are borne by animals, and the majority of sun mesophytes and xerophytes are wind distributed. In each group, however, are numerous exceptions to the rule, owing to migration into various types of habitats.

Influence of Seed Production.—The chances of migration depend, in a large degree, upon the number of fruits, seeds, or spores produced. A large seed production increases the movement of a mobile species. Seed production of a species bears a general relation to its power of invasion. The latter is expressed more exactly by the efficient seed production, which is the total number of fertile seeds left after the usual action of destructive agents. The number of seeds produced by a tree of limber pine (*Pinus flexilis*) is large, but the efficiency is almost nil. The toll taken by nutcrackers, jays, and squirrels is so complete that no viable seeds were found in hundreds of mature cones examined. In the case of two species with equally good devices for distribution, the one with the larger number of seeds is the more mobile. Even in immobile plants, seed production increases the few chances of movement.

The viability of seeds is greatest in typical many-flowered (polyanthous) species, such as grasses and composites, which produce but one seed per flower. This is shown by the large number of successful invaders, *i.e.* weeds produced by these groups. The movement of abortive seeds, of course, is of no benefit to the species. Fertility is often low in plants with many-seeded (polyspermous) flowers due to the lack of fertilization or to competition between the ovules, *e.g.* evening primrose (*Œnothera*).

The periodic variation in seed production is a factor of much importance, especially in trees and shrubs. This is due to the fact that birds and rodents consume practically the entire crop in the case of conifers, oaks, beech, etc., during poor seed-years. The efficient production is high only during good seed-years, and the invasion of such species is largely dependent upon the occurrence of such years.

Position of Disseminules.—The position on the plant of the part disseminated, that is, its exposure to the distributing agent, plays a part in mobility. In the majority of flowering plants, the position of the inflorescence gives a maximum of exposure, but in many cases special modifications are developed to place spores or seeds in a more exposed position. The height of the inflorescence from the ground or above the surrounding plants aids in increasing the distance to which the spores or seeds are carried in the first flight.

The most perfect device of this kind is found in such composites as the dandelion, prairie cat's-foot (*Antennaria*), etc., in which the stalk stretches up after flowering is completed. By the time the involucre expands to release the fruits, the flower stalk has often grown to several times its original length. The movements in fruits of various plants often serve to place seeds and fruits in a better position for dissemination. In certain composites, the involucral scales are reflexed at maturity, thus loosening and lifting the achenes. A somewhat similar result is obtained in such grasses as *Stipa* and *Aristida* by the twisting of the awns. In many mosses, liverworts, and puffballs, the spores are sifted out through slits or teeth, or the whole spore mass is elevated and held apart by the mass of elaters or threads. In most cup fungi, the spores are driven out of the cup by tensions within, caused, in some cases, by the sudden change of glycogen to sugars with a corresponding sudden increase in osmotic pressure.

Rôle of Migration Agents.—It is significant that the agents which carry migrules, *viz.*, wind, water, gravity, glaciers, man, and animals, are also initial causes of bare areas. Thus, the force which produces an area for succession also brings the new population into it. Often the two processes are simultaneous, especially in denuded habitats. Water as a migrating agent brings to new water or soil areas chiefly those germules which can be gathered along its course. Thus, it is evident that a new area with an excess of water will be provided, for the most part, with water-borne migrules and that the viable ones will practically all be of this kind. The action of wind is broader, but it is clear that initial areas due to wind are found only in wind-swept places, which are, of course, where the wind will carry the largest load of migrules. An extremely close connection is found also in talus slopes due to gravity, for the majority of the species are derived from above. The universal

prevalence of ruderals in denuded areas due to man's activities is sufficient evidence of the direct relation here.

Methods of Migration.—The possibility of migration depends primarily upon the action of distributing agents.[253] In the absence of these, even the most perfect modification is without value, while their presence often brings about the movement of the most immobile plants. As to method of migration, the following groups are distinguished:

Water.—This group comprises all plants distributed by water whether in the form of ocean currents, tides, streams, or surface run-off. In the case of streams and run-off especially, the nature of the modification is of little importance, provided the disseminules are impervious or little subject to injury by water. The action of water upon seeds, however, practically eliminates all but hydrophytic or ruderal species in water or wet areas, though this effect is doubly insured by the difficulties of ecesis.[151] The high-water stage following spring floods, is often marked by rows of seedlings. The same is true of the shores of ponds and lakes. The chief species are water, shore, and bottom-land plants. On newly formed islands, frequently water-borne plants are found on the margins and those transported by wind in the interior.[199,200,451]

The coconut, which is often seen floating on tropical waters, and which until recently has been cited as a classical example of long-distance water distribution, loses its viability within a few days due to water infiltration.[106,107] The seeds of certain hydrophytes, such as the arrowhead (*Sagittaria*), and the mermaid weed (*Proserpinaca*), have been shown to have retained their vitality after lying in mud covered with water for 7 years.[492] Motile plants, or those with motile cells, as well as submerged forms and unattached floaters, such as duckweeds (*Lemnaceæ*), belong entirely to this group.

An instructive example of ocean currents as agents of dispersal is afforded by the floras of the two types of mangrove forests. The eastern mangrove has a rich flora very uniform along the coasts of East Africa, India, and Malaya. The western mangrove has a poor flora, the important species being the same on the western coast of Africa and the east coast of tropical America. The two types have no species in common. Distribution throughout the two regions has been entirely by ocean currents. It has been shown that the mangroves and their associates of the western region are all capable of floating in the sea for at least 2 months and that all could be carried by the main equatorial currents from West Africa to South America. In the mangroves, the fruits are viviparous and it is the seedling which is carried.[201,494]

Wind.—The group of wind-distributed species includes practically all terrestrial plants in which modifications for increasing the surface of the seed or fruit have been greatly developed or in which the part carried is minute.[408] Sac-like, winged, hairy, parachute, pappose,

plumed, and some awned seeds or fruits are the various types of modifications for wind distribution. Whatever the device, the greater the surface exposed in proportion to the weight the more resistance it offers to falling through the air and the farther it may be carried by the wind. Milkweeds, thistles, willows, and dandelions increase the surface enormously without materially increasing the weight. The fruit of the dandelion is kept aloft indefinitely in a breeze of only 2 miles per hour.[495] The seeds of orchids and many ericaceous plants are as fine as particles of dust, the former often weighing only 1/500 milligram. These, like spores, rise into the upper currents of air and may travel hundreds of miles.

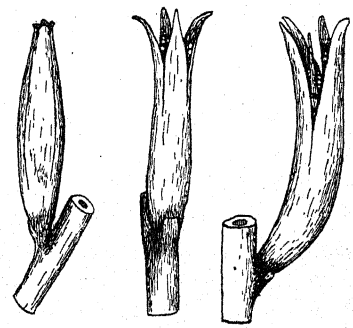

FIG. 71.—Three stages in the splitting of the capsule and dispersal of the seeds of an evening primrose (*Oenothera biennis*).

On the island of Krakatoa, whose vegetation was entirely destroyed by a volcanic eruption in 1883, the first plants were thallophytes and bryophytes from wind-blown spores. The first vascular plants to appear in abundance were ferns, whose spores are readily scattered by the wind. The distance to the nearest island not affected by the eruption is over 12 miles, and the distance to the coast

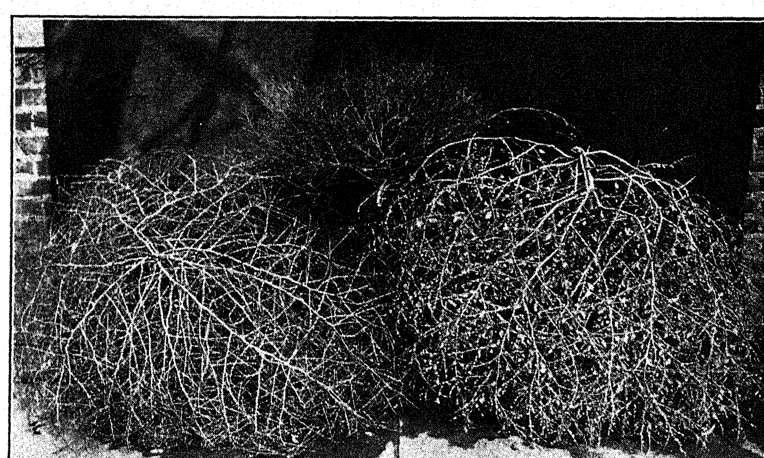

FIG. 72.—A group of tumbleweeds, Russian thistle (*Salsola pestifer*), left; winged pigweed (*Cycloloma*), center; and orach (*Atriplex hastata*). The largest is nearly 4 feet in diameter.

of Java is about 25 miles. Fifteen years after the eruption, 53 species of seed-bearing plants had reached the island. Of these, it was estimated that 60 per cent, chiefly shore forms, were brought by ocean currents, 32 per cent by wind, and 8 per cent by animals.[156]

Plates of gelatin exposed from airplanes at high altitudes collect spores of many fungi, including those of wheat rust and other disease-producing organisms.[510] The rapid spread of the chestnut blight (*Endothia*) throughout the range of the host within a few years is an excellent illustration of the efficiency of the wind as an agent in spore distribution.[230] Most epiphytes, whether lichens, mosses, ferns, or seed plants, such as orchids and bromelias, have wind-blown disseminules. The wind often plays an important rôle as migrating agent in shaking the stalks of plants with dehiscent fruits, such as evening primrose, and thus causing the seeds which are unmodified for transport to be scattered some distance from the parent plant (Fig. 71). In windswept areas, such as prairies and plains, many plants or inflorescences migrate for miles as tumbleweeds, scattering the seeds as they go. Such are Russian thistle (*Salsola*), tumbleweed amaranth (*Amaranthus græcizans*), species of *Atriplex*, old-witch grass (*Panicum*), fire grass (*Agrostis*), etc. (Figs. 72 and 73). The wind is the most efficient agent of migration but, at the same time, the most wasteful. Most of the migrules are carried to areas already so thoroughly populated that the newcomer can not ecize.

FIG. 73.—Tumbling panicles of fire grass (*Agrostis hiemalis*) left, and old-witch grass (*Panicum capillare*).

Animals.—Animals distribute seeds in consequence of attachment, carriage, or use as food. Dissemination by attachment has been specialized to a high degree. The three types of contrivance for this purpose are found in spinose, hooked, and glandular or gelatinous coated seeds or fruits. Distribution by ingestion and that by carriage often plays a striking part on account of the distance to which the seeds may be transported.[36] The one is characteristic of fleshy fruits and the other of nut fruits. The destructive action of seed-eating animals, particularly birds and rodents, is often completely decisive. So complete is the destruction of seeds in certain instances, notably in forests of lodgepole pine, that the appearance of certain species is possible only where the rodent population is driven out or destroyed. This is confirmed by the almost uniform failure of broadcast sowing in reforestation, as well as in other methods of sowing when the birds and rodents are not destroyed. In a single squirrel cache, 4 or 5 bushels of cones are often found, and in years of good seed production, sometimes as many as 15.[295] Foresters have practically abandoned seeding and now reforest or afforest areas

by means of transplants grown in nurseries.[548] The destruction of seed is a factor of great importance affecting invasion.

Distribution of species by animals is often more efficient, since each species of animal usually frequents a certain type of vegetation. The usual way for such trees as walnuts, hickories, and oaks to migrate is by animal carriage. Nearly all may be eaten, but some, buried in the forest or near its margin, are overlooked. Most forest animals seldom venture far into grassland; neither do prairie animals usually frequent woods. The rapid spread by birds of shrubs and vines with edible fruits to planted groves is common.[398] Some birds may carry small seeds from one marsh to another in the mud on their feet or feathers. If the seed or fruit has a mucilaginous coat, such as certain species of *Juncus* and others, these may adhere to their feathers.[201] Mistletoe, a parasite, often of considerable economic importance on trees, is disseminated by birds. After eating the enveloping fleshy rind, the slimy seeds which frequently stick to their bills may be wiped off upon the limbs where they are perched and, hence, in places suitable for germination.[231,386] Certain seeds with oily or albuminous appendages are often distributed by ants, *e.g.* wild ginger (*Asarum*), bloodroot (*Sanguinaria*), etc.[576]

Man.—Distribution by man has no necessary connection with mobility. It acts through great distances and over immense areas, as well as near at hand. It may be intentional, as in the case of cultivated plants, or unintentional, as in thousands of native and foreign species. Ships carry the migrules over the oceans, and trains and automobiles scatter them over the land. Wagon trails through the prairies were lined with ruderals. More than half of our weeds have been introduced from Europe by the continual shipment of agricultural and horticultural products.

Gravity.—Gravity is an agent of migration in hilly and mountainous regions, where seeds and fruits regularly reach lower positions, either by falling from bank, cliff, or rock or, more frequently, by the breaking away and rolling down of rock or soil masses. In this process, nearly always, large quantities of seeds are destroyed. Dissemination by this method is necessarily local, though it plays an important part in rock fields and gravel slides of mountains, especially in the case of immobile species.

Glaciers.—Transport by glaciers is of slight importance at the present time, because of their restriction to alpine and polar regions where the flora is poorly developed. In considering the migrations of the glacial epoch, however, distribution by glaciers is an important factor.

Growth.—The mobility of species disseminated by the growth of offshoots is extremely slight and the annual movement relatively insignificant. Solomon's-seal (*Polygonatum*), strawberries (*Fragaria*), and sumac (*Rhus*) are examples. The certainty of migration and ecesis is

so great, however, and the presence of offshoots so frequent in terrestrial plants that growth plays an important part in migration in the local communities. They produce mass invasions such as cattails into ponds and shrubs into grassland, which are very effective.

Propulsion.—Dissemination by mechanical propulsion, though it operates through very small distances, is important on account of its cumulative action from year to year. The number of plants with contrivances for propulsion is very much smaller than the number of those with offshoots. All species of this group agree in having modifications by which a tension is established. At maturity this tension suddenly

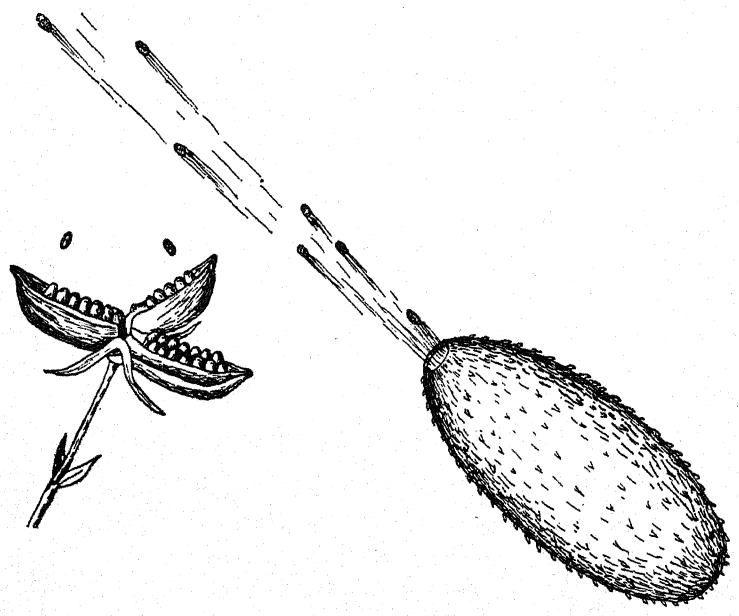

FIG. 74.—Fruits of violet (*Viola elatior*) and squirting cucumber (*Ecballium elaterium*) discharging their seeds. (*Redrawn from Kerner and Oliver.*)

overcomes the resistance of sporangium or fruit and throws the enclosed spores or seeds to some distance from the parent plant. In accordance with the manner in which the tension is produced, sling fruits are classified as follows:

1. Hygroscopic Fruits.—These include the ferns, in which the sporangia dehisce in a somewhat complicated manner. A ring of dead tissue, the annulus, springs back suddenly and releases the spores when a certain degree of desiccation is reached. The sporangia are elevated on foliage leaves or special stalks and the minute spores are often carried great distances by the wind.

2. Turgescent Fruits.—Propulsion by turgescence occurs in a large number of fungi. *Sphærobolus*, for example, by a sudden change of

glycogen into maltose and other sugars in its sporangium becomes so turgid that by a sudden release in the tissues the tiny spore masses are hurled for a distance of many feet.[551] In the touch-me-not (*Impatiens*), the five somewhat fleshy valves of the capsule possess a layer beneath the epidermis which has an elastic wall and a very high turgor pressure. As the fruit ripens, the valves become separated from the internal septum and are held together only very slightly so that they are liberated by the slightest touch or breeze. When this occurs, each valve rolls inward like a watch spring with such force as to whip out the seeds, which are thus scattered some distance. The squirting cucumber (*Ecballium*) forcibly ejects the seeds because of turgidity within the fruit (Fig. 74). *Oxalis* is another example of a fruit expelling its seeds because of increased turgidity.[278]

3. Dry Fruits.—The number of fruits which dehisce upon drying is very large but only a small number of these expel their seeds forcibly. The hygroscopic movements of the teeth of mosses and flowering plants, such as many of the pink family, are of interest. Often, the teeth curve back and open the capsule in dry weather, while in moist or rainy weather they quickly bend up and close the entrance. Thus, the germules escape only under conditions favorable to their being thrown some little distance. In violets, when the pods ripen, the carpels press harder and harder on the smooth seeds held in an angle between them; when, suddenly, the pressure overcomes the friction, the seeds are shot to a distance of several centimeters in a manner similar to that in which one may shoot a bean by pressing it between the thumb and finger (Fig. 74). In the geranium, the carpels separate from the base of the main axis and curl upward with such suddenness as to discharge the seeds (Fig. 75). The sharp explosion of the bursting witch-hazel fruits is a familiar autumn sound in an eastern forest, the seeds being hurled violently a distance of several meters.

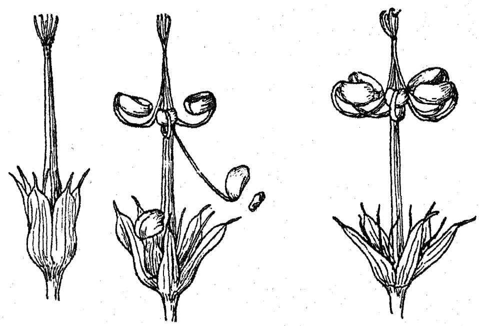

FIG. 75.—Three stages in the ripening of the fruit of geranium (*Geranium richardsonii*).

Other ways in which drying brings about the sudden splitting of fruits are illustrated by certain mustards (*Erysimum*) and *Lotus*.

4. Mortar Fruits.—In some plants, especially composites, borages, and mints, the achenes or nutlets are so placed in the persistent involucre or calyx that the latter serves as a kind of mortar for the projection of the seeds when the stem is sharply bent to one side by any force such as the wind or some animal.

Agents of Migration.—Make a careful survey of the plants found in an isolated community, such as a grove or thicket surrounded by grassland. Classify them in accordance with the agent that has probably brought them into the area. What is the nearest station from which the fleshy fruits of the various trees, shrubs, and herbs might have been carried? Complete the study on page 101 by adding the probable agent of migration after each of the species listed.

The Direction of Migration.—The direction in which a migrant moves is determined by the agent concerned. While migration tends to radiate in all directions from the parent group, as illustrated by the action of winds which blow from any quarter, it often becomes more or less *determinate* (Fig. 76). In the case of constant winds, for example, it is somewhat definite, the exact direction being determined largely by the fruiting

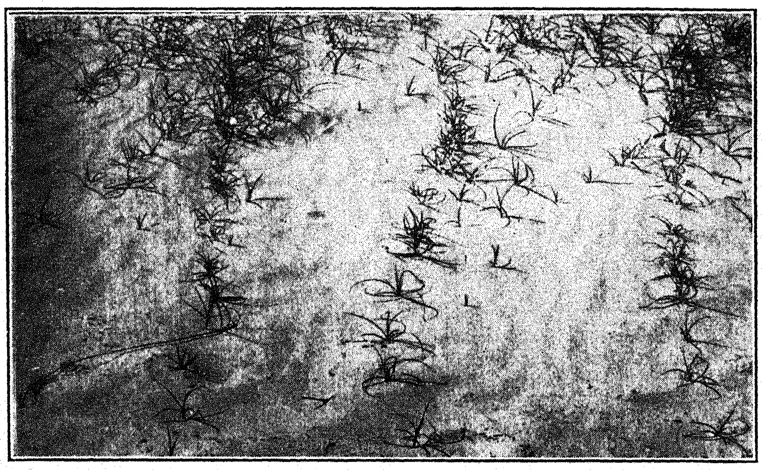

Fig. 76.—Linear migration of a sedge (*Carex arenaria*) on a sand dune.

period of the species concerned. The migration of plants along water courses is an excellent example of determinate migration. The position of invaders with reference to the original home does not necessarily indicate the only direction of migration, since seeds are regularly carried to places in which they can not ecize.

In general, migration is *radial* or *indeterminate* when it is local and *unilateral* or *determinate* when more general. The local movement of plants carried by animals takes place in all directions, while their distant migration follows the pathway of migratory birds or mammals. Distribution by man is determinate when it takes place along commercial routes or highways. In ponds, lakes, or other bodies of standing water, migration usually occurs in all directions, but in ocean currents and streams it is determinate except for motile species. Dissemination by gravity and glaciers is local and definite, but propulsion is entirely indeterminate. Migration by growth is equally indefinite, but it produces a

radiate movement away from the parent mass, while propulsion throws germules into the mass as well as away from it. Distant migration may take place by means of water, wind, animals, and man, and it is, in some degree, determinate, since these agents act in a definite direction over great distances. On the other hand, local migration is indeterminate, as a rule, except in the case of streams, glaciers, and slopes. The direction of migration is thus seen to be controlled by the distributive agent. The distance is determined by the intensity and duration of the agent as well as by the nature of the area through which it acts.

In succession, local migration is primarily responsible for the population of new areas. Nearly always, effective invasion in quantity is local. Forest and shrubs usually extend their areas slowly, working out from their margins. When migrants travel long distances, they are apt to be too scattered to become controlling. This undoubtedly holds true for the great migrations following glacial invasions where populations of tundra, grassland, and forest moved hundreds of miles. They were apparently only the gross result of repeated local movements, acting in the same general direction through long periods.

If the germules arrive too soon, that is before the habitat is suitable for their growth, *e.g.* seeds of trees on moss-covered rocks, migration is entirely ineffective. The same holds true after the sere has passed into a stage of development so that the habitat is unsuitable for their growth. To modify the course of succession, migration must be followed by ecesis.

ECESIS

Ecesis is the adjustment of the plant to a new home. It consists of three essential processes, germination, growth, and reproduction. It follows migration and sooner or later results in competition. Ecesis comprises all the processes exhibited by an invading germule from the time it enters a new area until it is thoroughly established. Hence, it really includes competition, except in the case of pioneers in bare areas. The germination, growth, and reproduction of a plant growing among others are the same as those of an isolated individual except that those of the former take place under conditions modified by the neighboring plants. Hence, it will be clearer if ecesis is considered first and competition subsequently.

Ecesis is the decisive factor in invasion. Migration without it is wholly ineffective. In fact, migration is usually measured by the number of plants that ecize in an area rather than by counting the germules that have arrived. The relation between the two is most intimate. Migration, if followed by ecesis, results in the establishment of a new center from which further migrations may occur, and so on.

The time of year in which fruits ripen and migration occurs has a marked influence upon the establishment of a species. Seeds which

ordinarily pass through a resting period are often brought into places where they germinate at once and perish because of unfavorable factors or because competing species are too far advanced. Spores and seeds capable of immediate germination may likewise be scattered at a time when conditions make growth impossible. The direction and distance of migration are decisive because the seed or spore is carried either into a habitat sufficiently like that of the parent to secure establishment or into one so dissimilar that germination is impossible or at least is not followed by growth and reproduction. The rapidity of migration has little influence except in cases of conidia, gemmæ, etc., which have not

Fig. 77.—Migration and germination of great ragweed (*Ambrosia*) in cracks in soil of a river bank.

much resistance to drying. The number of migrants is likewise important since it affects the chances that germules will be carried into bare areas where ecesis is possible. Willows, for example, may colonize a new channel deposit if the wind carries the seeds to the new area which is much like that of the parent one, in sufficient numbers, within the few weeks before they lose their viability. They must be carried at the right time, in the proper direction, and a sufficient distance, with enough rapidity, and in large numbers. Thus, each of these factors plays an important part.

In unattached aquatic forms, *e.g.* algæ, water hyacinth, etc., the growing part or plant is usually disseminated, and ecesis consists merely in being able to continue to grow and reproduce. It is quite certain because of the similarity of aquatic habitats. In dissemination by off-

shoots, the conditions are somewhat similar, and ecesis consists of growth and reproduction alone, since the offshoot grows under the same conditions as the parent plant.[542]

Ecesis occurs only when a migrant enters a new place in which it germinates, grows, and reproduces. Plants may migrate into an area without germinating; they may germinate and then disappear; they may germinate and grow without reproducing; or they may complete ecesis by reproducing either by flowers or by offshoots or both (Fig. 77).

Germination.—The first critical process in ecesis is germination. Germination may be regarded as the appearance and unfolding of the first leaf or leaves which may or may not be cotyledons. The seeds of some species of *Oxalis* germinate soon after leaving the capsule, and in viviparous plants (*e.g.* mangrove) the embryo continues in a state of uninterrupted development from the outset. Others, like the willow and cottonwood, retain their power of germination for only a few days. But even when conditions of moisture, temperature, and oxygen supply are favorable, the overwhelming majority of seeds lie dormant for a few months and at least until the growing season following their formation.

Dormancy and Delayed Germination.—When a seed does not germinate immediately upon leaving the parent plant, it is said to be in a state of dormancy. Dormancy is not confined to seeds, however, but is also characteristic of many offshoots such as rhizomes, bulbs, tubers, etc.[138,140] Dormancy may extend over a period of only a few days or weeks as in the seeds of the elm, cottonwood, and willow, which do not withstand desiccation, or it may persist for years as in certain legumes, mints, and snapdragons. It is usually more pronounced in seeds produced in late summer or autumn.

Dormancy is much more general among native than among cultivated plants. Frequently, the latter show none, and under favorable conditions their seeds will germinate before leaving the parent plant, *e.g.* wheat in the shock. Wild oats (*Avena fatua*) and cultivated oats (*A. sativa*) both produce seed in summer. Unless artificially stored, the latter germinates at once, and upon the advent of cold weather the crop is frozen. The wild oats lies dormant, but germinates the following spring. Man, by his methods of seeding and harvesting, has unintentionally selected plants the seed of which germinate readily, since only those seeds that germinate soon after sowing mature plants for harvest. Thus, throughout the centuries of agriculture those races of plants that did not germinate readily were largely eliminated. The causes of dormancy are many. Some of them lie within the seed, others are due to the external environment.

External Causes of Dormancy.—When seeds mature in late autumn, the temperature may be too low for germination. Or the temperature at the time of seed ripening may be too high, as in the case of cool, temperate species growing in the desert. In fact, at ordinary summer

temperatures, many seeds will not germinate but remain dormant until death overtakes them.[2,215] Lack of a sufficient water supply is another common cause. On the Great Plains, fall-sown wheat often fails because of drought to germinate until spring. An insufficient supply of oxygen may prevent germination, as when seeds upon ripening fall to the bottom of a pond. Frequently, they are covered with earth to such a depth that a supply of oxygen is practically excluded. Here they may lie dormant for long periods and germinate only upon being brought to the surface.[128]

On an area planted to woodland, seeds of certain mustards and plantain lay dormant for 20 to 40 years before finally producing seedlings

Fig. 78.—Reproduction of Douglas fir in Washington from seed stored in the forest floor. (*After Hofmann.*)

Ten years after tilled land had been sown to pasture, the sod was again broken. This resulted in the germination of 16 species of weeds that had lain dormant.[48] Where seeds have been buried at a depth of 3 feet in open bottles in moist sand for a period of 40 years, 10 out of 22 species remained viable.[134] Seeds of many land plants have been shown to lie dormant in mud covered with water for a period of several years. Where abundant organic matter is decaying in the soil, so much carbon dioxide may be evolved as to delay germination.[279] This may occur in garden or forest soils or where the oxygen supply is low, as in the mud of ponds. It is a notable fact that when a forest is cut over or burned, many seeds which have found conditions unfavorable for germination, rapidly produce seedlings (Fig. 78). Temperature, water content, and oxygen supply may all be involved.

The seeds of a few species, *e.g.* bluegrass, certain varieties of tobacco, mistletoe, and mullein, will not germinate in the absence of light or at least germinate better when illuminated.[127] The cause of dormancy in many such cases has been found to be complicated with other factors such as temperature, nitrogenous compounds, or enzymes. Light probably alters the seed coat in relation to its permeability to water or oxygen.[177]

Thus, the control of the habitat is twofold. It determines whether the seed will germinate immediately or during the season. If germination is delayed, it determines whether or not conditions will permit the seed to remain dormant but viable for several years. Habitats which are most favorable to germination are least favorable to dormancy, and, conversely, those which allow seeds to persist long periods are inimical to germination. In many cases, of course, the surface layer favors germination, and deeper layers promote dormancy.

Internal Causes of Dormancy.—The failure of seeds to germinate under favorable external conditions is often due to certain characteristics of the seed or fruit coats or of the embryo.[130] The more important causes are as follows:

Seed Coats Impermeable to Water.—One of the commonest causes of dormancy is the exclusion of water from the seed because of the impermeability of the seed coat or ovary wall. Many water-plants such as *Nelumbo*, mints, and legumes are examples of this type. This character, however, is not peculiar to any particular group. In some species, all of the seeds are "hard" and impervious to water; in others, only some of them. Since no absorption takes place even when the seeds come in contact with water, germination can not occur until the seed coat is made permeable. This may be brought about by a natural, slow deterioration of the seed coat or artificially by abrading or removing it. The former agencies, such as freezing and thawing and bacteria and fungi, may require a period of several years. Naturally, when a crop of alfalfa or clover is sown, it is advantageous to have all of the seeds germinate at about the same time. It not only requires less seed, but also competition with weeds is much reduced and a crop ripening evenly is the result. Hence, the seed coats are usually abraded or scarified mechanically, thus greatly increasing the percentage of germination although the vigor of the seedling is sometimes decreased. Small lots of seeds may be treated with acids or alkalies or the coats abraded by stirring them vigorously with sharp sand. Heating the seeds, *e.g.* alfalfa, to a high temperature (85° to 90°C.) not only increases permeability to water and increases germination but also, at the same time, kills many of the accompanying seeds of weeds.[325,509]

Effect of Impermeability of Seed Coat on Germination.—Select 12 fully matured seeds of the previous year's crop of honey locust (*Gleditsia*) or Kentucky coffee tree

(*Gymnocladus*). Cut through the seed coats of 5 of the seeds with a file and place with 5 others in a glass of water, saving 2 for a check on size. Change the water and examine from day to day for a week and state results. From a lot of unscarified seed of sweet clover (*Melilotus*) or alfalfa (*Medicago*), select 50 that are well developed and a similar number from the same lot after they have been scarified. Place them in a moist chamber on wet blotting paper. Count and remove those that have germinated each day for a period of 10 to 14 days.

Seed Coats Impermeable to Oxygen.—In a second class of seeds, dormancy is due to the exclusion of oxygen. The seed coats or fruit coats enclosing the seeds are either impermeable to oxygen or at least do not permit it to diffuse into the embryo in sufficient amounts to promote germination. This is the cause of dormancy, as may be readily shown in the case of the cocklebur (*Xanthium*), either by injuring the seed coat, by increasing the oxygen pressure, or, more simply, by removing the coat.[491] The same agencies that cause hard seed coats to become permeable to water also gradually reduce the impermeability of seed coats to oxygen. Many grasses, composites, and other plants belong to this group.[488] Subjection to a high temperature (120°F.) for a period of time increases the permeability and breaks the dormancy.

Seed Coats Mechanically Resistant.—In other cases, water and oxygen can be absorbed, but only a small amount of water enters the seed since the expansion of the embryo is limited by the seed coats. In water plantain (*Alisma plantago*), for example, the embryo swells and presses against the restraining walls with an imbibition force of about 100 atmospheres but can not rupture them and is thus unable to germinate.[129] The seeds of black mustard (*Brassica nigra*), shepherd's-purse (*Bursa bursa-pastoris*), peppergrass (*Lepidium*), and pigweed (*Amaranthus retroflexus*) belong to this class. These may lie dormant in the moist soil for many years, although if brought to the surface the seed coats more readily decay. This explains why they are such persistent weeds in fields and in gardens, occurring even in those that have been kept free from weeds for a number of years. When cultural operations bring the seeds to the soil surface where conditions are favorable for germination, they immediately produce a crop of seedlings. Likewise, seeds of many water plants, such as arrowheads (*Sagittaria*), pondweeds (*Potamogeton*), bur reed (*Sparganium*), etc., may lie dormant in the mud for many years, the resistance of the fruit walls to embryo expansion being the chief cause, though oxygen relations may sometimes be involved.

Imperfectly Developed Embryos.—In some seeds, the embryo is not completely formed when separation from the parent plant occurs. In some cases, it is little more than a fertilized egg, and all gradations from these few-celled embryos to nearly or completely developed ones may occur. In certain plants indeed, such as *Ginkgo*, under cultivation in Europe, fertilization does not take place till after the seed has fallen.

In others, development of the undifferentiated embryo proceeds slowly in the detached seed through autumn and winter and is completed just before germination in spring. Plants belonging to this general group are dogtooth violet (*Erythronium*), buttercup (*Ranunculus*), many orchids, and holly (*Ilex*).

Embryos Requiring Acidity.—Certain seeds with fully developed embryos fail to germinate even when the seed coats are removed and they are placed in an environment ordinarily suitable for germination.[413] This type of dormancy is due to lack of acidity and until the proper degree of acidity is developed or artificially supplied, the seeds will not germinate.[430] In the hawthorn (*Cratægus*), for example, this after-ripening process requires 1 to 3 months, the acidity of the embryo increasing as after-ripening proceeds. This may promote water absorption and affects metabolism, particularly enzyme activity, which is essential in the processes of digestion, assimilation, and respiration.[150] The seeds of many plants belong to this group.[216] Conspicuous among them are red cedar, hard maple, peach, linden, apple, and ragweed. Such seeds may be germinated at once by removing the seed coats and immersing the embryos in a weak acid.[376] A rather low temperature (about 40°F.) is generally favorable to the development of acidity and explains why seeds that are layered, *i.e.* placed under a thin layer of soil out of doors during winter, germinate much sooner than those kept at room temperature. Layering is a long-established horticultural practice. Much more work must be done to devise good methods of germinating seeds and producing seedlings from many of even the most common horticultural plants.[602]

Longevity of Seeds.—Little is known about the normal period of viability of seeds under the usual conditions of natural sowing.[194] When the seeds are thoroughly dried and stored in a dry place, they may retain their viability for a long time. High temperature hastens loss of viability. Seeds of most cultivated plants rapidly decrease in germinating power after only 1 or 2 years. Seed corn, for example, is usually selected from the current year's crop. As a rule, the seeds of many native species remain alive at least 5 to 10 years and a few may, under favorable conditions, lie dormant 25 to 50 years.[28,37] Legumes, water lilies, mallows, and mints are especially long lived.[157] There are a few authentic records of some seeds germinating after being stored 100 years, and *Nelumbo nucifera* gave 100 per cent germination after lying for more than 200 years in moist peat. But seeds germinating after long periods of dormancy are rare.[372] Hard-coated seeds are especially long lived. During prolonged storage the proteins of the seed are gradually coagulated or changed into insoluble forms. Hence, when the seeds are planted the proteins do not become soluble nor will the seeds grow.[127]

It has been seen that the germination is postponed in a variety of ways and the vitality of the seed retained over a long period of time.

The longevity of a seed combined with dormancy is a means by which the offspring of a single parent or the seeds of a single year may go on germinating throughout a series of years. This may be a real advantage inasmuch as some of the germinating seeds may find conditions favorable for growth and reproduction. If all germinated at the same time, all might be lost because of drought or cold or for other reasons.

Rate of Germination.—The germinative power of the seeds of forage plants in Oregon has been determined. Both those of the high mountain and lower ranges were tested. Germination was affected by both altitude and slope and by the vigor of the plant, those weakened by overgrazing producing less viable seed. Seed viability decreased with altitude. Species of the higher ranges (above 6,500 feet) gave an average germination of 28 per cent; those at lower elevations, 45. In general, the more weedy species gave a higher percentage of germination than the more desirable forage grasses.[432]

Experiments with a large number of prairie species show that the amount of viable seed produced varies greatly from year to year. This may depend, in part, on environmental conditions during the time of flowering (*anthesis*), while, in some cases, viability is greatly reduced by the occurrence of frosts before the seeds of late-blooming species have sufficiently ripened. Extreme variation was from 84 to 0 per cent germination in one species, the prairie false boneset (*Kuhnia*), during two seasons. Germination of 20 to 25 per cent was considered good and 10 to 15 per cent was usual.[98,259,354]

Extended experiments among cultivated, annual crops show that large, well-developed seeds often give a higher percentage of germination and greater yield than smaller ones.[599] Similar relations probably hold true for native plants.

Depth of Germination.—Successful germination usually occurs only at the proper depth, with the exception of bare areas with wet or moist surfaces. A few species have the peculiar property of being able to plant themselves when they germinate on the surface, but the rule is that seeds must be covered with soil to permit ecesis. This is particularly true of seeds on a forest floor covered with a thick layer of leaves or needles, which prevent the root from striking into the soil. There is, doubtless, an optimum depth for each species, which varies more or less with the habitat. Too great a depth prevents the seedling from appearing altogether or causes it to appear in such a weakened condition that it quickly succumbs. In the former case, it may lead to dormancy and germination only after the area has been cleared or burned.

The effect of depth of planting and its relation to the size of seed has been shown as follows in the case of conifers;[242] the relative size of the seeds is shown in Fig. 66.

TABLE 1.—GERMINATION AND ESTABLISHMENT IN RELATION TO DEPTH OF PLANTING

Species	Depth of planting, inches	Per cent germinating	Per cent appearing aboveground
Yellow pine (*Pinus ponderosa*)	1.00	82	82
	4.00	36	0
Douglas fir (*Pseudotsuga mucronata*)	0.50	93	93
	4.00	17	0
Western hemlock (*Tsuga heterophylla*)	0.25	96	96
	1.25	42	0
White cedar (*Thuja plicata*)	0.12	78	78
	1.00	26	0

It was also found that the seeds of conifers lie dormant in the forest soil for a period varying from 3 years in hemlock to 6 in white pine (*P. monticola*) and Douglas fir, and those of the yew (*Taxus*) for 8 years. These data throw much light upon the source of seedlings following lumbering and burning. In many parts of the West, where a single fire has destroyed the mature forest, the natural restocking has been prompt, uniform, and complete. But after the seeds in the forest floor have germinated and fire again occurs before the trees reproduce, the area must be artificially reseeded. In other cases, reproduction from seed deposited in the duff can not be depended upon.[301] In lumbering, it is a common practice to leave three or four large coniferous trees standing on each acre to insure the scattering of seeds throughout the area.[532] This is in striking contrast to cut-over hardwood areas where oaks, hickories, and other deciduous trees sprout vigorously from the stumps which retain this power of propagation for many years.

Experiments with prairie species showed that depth of planting has a pronounced effect upon germination and establishment. With the grasses, a depth exceeding 0.5 to 1 inch was distinctly detrimental, except in the needle grasses (*Stipa*) which plant the seed deeply by means of hygroscopic awns. Most of the grasses, as well as the composites, did best at a depth of 0.12 to 0.25 inch.[98]

Effect of Depth of Planting upon Germination and Establishment.—Secure viable seed from three or more native plants including a grass, a legume, and a composite. Plant the seed at various depths so as to determine the best depth for maximum germination and establishment. Use loam soil in good tilth and water daily, if necessary, especially those cultures where the seeds are shallowly planted. Is there any relation between depth of planting and size of seed?

Fate of Seedling.—The crucial point in ecesis is reached when the seedling is completely free from the seed coat and is thrown upon its own resources for food and protection. Even before this time, invading seedlings are often destroyed by birds and rodents, which pull or dig them

up for the food supply still left in the seed coats. The tender seedlings are often eaten by the smaller chipmunks, and sometimes coniferous seedlings seem to be pulled up or bitten off in mere wantonness. In farm practice, rows of corn may be missing for some distance due to the work of gophers and squirrels. Flocks of crows also do great damage. In regions where overgrazing occurs, the destructive action of animals is very great, especially in the case of sheep, although this may be partly offset by their planting of seeds. Some toll is taken by damping-off fungi, such as *Pythium* and *Fusarium*, in moist, shady soils, but these are, perhaps, never decisive except under artificial conditions.[223]

In the case of herbs, the greatest danger arises from excessive competition, especially in the dense aggregation typical of annuals. For example, in one experiment involving 3 square meters and 31,500 seedling great ragweeds (*Ambrosia trifida*), less than 400 plants (1.2 per cent) reached maturity. The direct effect is often due to lack of water, although light frequently plays an equally important part. Many attempts have been made to reseed the more arid, sparsely vegetated range lands to cultivated plants. Nearly all of the trials ended in failure, due to deficient soil moisture, lack of proper depth of planting, or suitable seed. On mountains or semihumid lands throughout the West, the results were partially successful. The seed was sown broadcast and usually worked lightly into the soil or trampled in by sheep. The most drought-enduring species such as Hungarian brome grass ranked among the first in the successful seeding, which, in some instances, reached 60 per cent. Naturally, the best results were obtained in the less arid portions of the area. Drought, lack of success in competition with the native species, and overgrazing were among the chief causes of failure.[431,437]

Seeds of prairie species sown on the soil surface during a period of several years gave a slightly higher percentage of germination and establishment in mixed prairie than in true prairie or short-grass plains. The number of species showing some germination was 79, 76, and 45 per cent in the above sequence, respectively. The annual precipitation at the several stations in the same order is 23, 28, and 17 inches. The establishment of the seedlings, however, was only 14, 9, and 11 per cent. The differences were due partly to water relations but largely to soil structure, the soil at the true prairie station becoming quite hard and cracked upon drying. Where the same kinds of seeds were planted at the proper depth in small, denuded areas, germination decreased with rainfall, being found among 85, 59, and 21 per cent of the species, respectively. Of these, 27 per cent became established in true prairie, 21 per cent in mixed prairie, and none in the short-grass plains.

Even a short period of drought after germination is often disastrous. Another critical period especially for grasses is that of tillering when the transpiring surface is rapidly increased. Simultaneously, new roots

appear. Unless the surface soil is moist, these can not absorb, and the plant is literally holding to life by a single thread. Mortality at this time is often very great[98] (Fig. 79).

With the seedlings of woody plants, the cause of greatest destruction is drought in midsummer or later. This is the primary factor in limiting the ecesis of many conifers, though the "heaving" action of frost is often great or even predominant.[203] The root system is often inadequate to supply the water necessary to offset the high transpiration caused by conditions above the surface of the soil. It is, moreover, too short

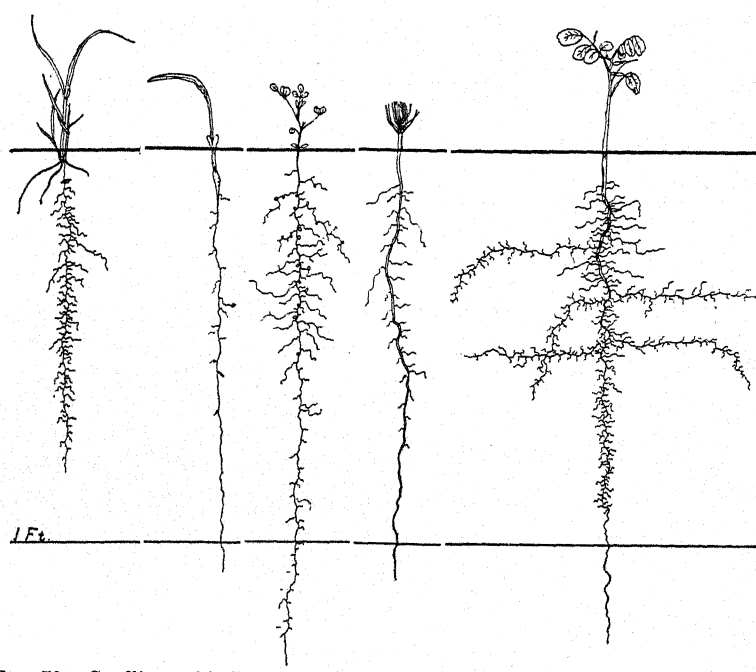

FIG. 79.—Seedlings of hairy grama (*Bouteloua hirsuta*), blazing star (*Liatris punctata*), sweet clover (*Melilotus alba*), western yellow pine (*Pinus ponderosa*), and black locust (*Robinia pseudacacia*). The grass is 44 days old, the sweet clover 63 and the rest 75.

to escape the progressive drying of the soil itself. In open places in the Rocky Mountains, such as parks, clearings, etc., the late summer mortality is excessive, often including all seedlings of the year. On the forest floor itself, it is considerable or even decisive in places where a thick layer of dry mold or duff increases the distance roots have to penetrate. Following destructive forest fires in the Rocky Mountain region, in 1910, nearly 3,000 acres of forest were seeded broadcast and over 10,000 acres by hand corn planters. Various native species were used. So great was the toll of drought, frost heaving, fungi, cutworms, etc., that the result was absolute failure in practically all cases.[548] After years of such experiences, the conclusion has been reached that the only dependable

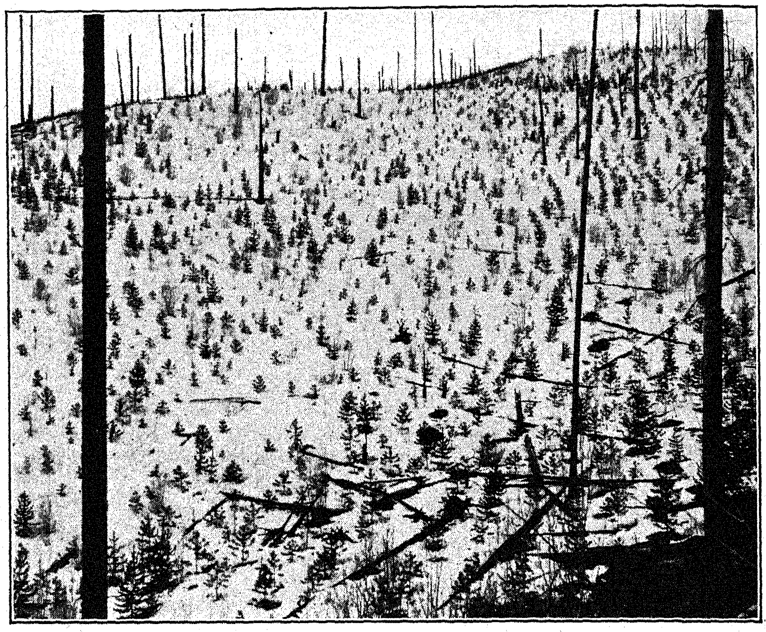

FIG. 80.—Western yellow pine plantation, 11 years old; Lolo National Forest, Montana. (*U. S. Forest Service.*)

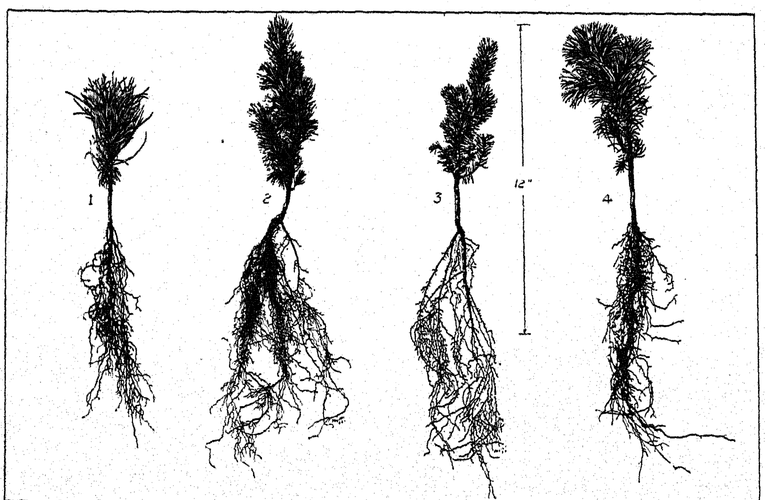

FIG. 81.—Typical development of lodgepole pine, blue spruce, Norway spruce, and western white pine grown in a forest nursery in Utah. The seedlings are grown two or more years in the seed bed and then usually one year in the transplant bed before they are transplanted in the field. (*After Korstian, U. S. Forest Service.*)

way of getting new forest crops started on denuded forest lands is to transplant seedlings of well-developed 2- or 3-year-old nursery stock[295] (Figs. 80 and 81).

In deserts, seedling mortality is very high. In the case of the paloverde (*Parkinsonia*), a leguminous tree in the deserts of Arizona, it was 89 per cent during the first 16 months and 97 per cent at the end of the third year.[478,485]

Growth.—Growth is the second stage in ecesis. If the seedling establishes itself, it is fairly certain that it will develop. This seems to be the usual result with herbaceous plants, though there are some exceptions in the case of trees and shrubs. Even though conditions become more extreme, the old plant is usually better able to resist them. Since the water relation is often decisive, the rate of root development and the distribution of roots in the deeper, moist soil is extremely important. Roots often grow at the rate of 0.5 to 1 inch per day, and even seedling grasses, trees, and other plants have remarkably extensive root systems. Light may be an equally important factor, but once the seedling is established it usually is able to endure much shading. In the case of woody plants, seedlings are notably tolerant of shade when contrasted with their demands later in life.

With increasing size of individuals, the demands become correspondingly greater. Hence, growth causes an increasing competition. Out of this competition some species emerge as dominants, reacting upon the habitat as regards light, water, nutrients, etc., in such a controlling way as to determine the conditions for growth of the other species in the community. Others represent an adaptation to conditions caused by the dominants and always play a subordinate part. This is well illustrated in the development of forests. The growth of shrubs and herbs on the forest floor is held in check because of the reduced light. A third behavior is shown by those species or individuals ordinarily capable of becoming dominants in some stage of the sere (*e.g.* bur oak in linden forest) when they appear tardily or reproduce under unfavorable light intensities. The growth is diminished and the plant becomes suppressed. In forest and thicket, suppression increases from year to year and usually results in death, either through the low photosynthetic rate or in consequence of the attacks of insects or fungi. While suppression reduces the normal development of the plant, often causing it to become tall, spindling, and poorly rooted, its most important effect lies in inhibiting reproduction.

Reproduction.—The invasion of a bare area is made possible by reproduction or seed production in the neighboring communities. The duration of each stage in the resulting sere is the consequence of the excess of reproduction over immigration of other species. Mosses, for example, dominate a rocky outcrop only as long as they reproduce more abundantly

than other invading species are able to do. Reproduction is consequently the final measure of the success of ecesis. In terms of succession, at least, ecesis occurs only when a species reproduces itself, and thus maintains its position throughout the stage to which it belongs. In the case of annuals, clearly there is no ecesis without reproduction, although they may appear and disappear finally in a single season. Even among perennials, there are few species that can maintain themselves in an area by vegetative propagation alone. Since bare areas are rarely invaded by means of vegetative propagation, complete ecesis in them must rest upon reproduction.

Ecesis in Bare Areas.—The bare area shows a selective action upon the germules brought into it. This is exerted by ecesis, for only those plants adapted to the conditions of the particular bare area, *e.g.* soil, water, rock, can ecize. The essential nature of such areas is found in their water relations. The two extremes for ecesis are water and rock. The first is impossible for plants whose leaves live in the air and light; the latter, for those whose roots must reach water. The plants which can ecize in such extremes are restricted in number and specialized in character but they are of the widest distribution, since the habitats in which they can grow are universal. From the standpoint of ecesis, succession is a process which brings the habitat nearer the optimum for germination and growth and thus permits the invasion of an increasingly larger population. Primary successions are long because the physical conditions for growth are, for a long time, too severe for the vast majority of migrants as well as for the rapid increase of the pioneers. Secondary soils such as abandoned fields, burns, etc., afford more or less optimum conditions for germination and ecesis. They are invaded and stabilized with corresponding rapidity.

CHAPTER VII

COMPETITION AND INVASION

The coming together of plants in the processes of aggregation, migration, and ecesis results in competition. When a plant is carried into a group of other plants or is surrounded by its growing offspring, the struggle which results between the individuals is competition. This movement of a plant or a group of plants from one area into another and establishment in the new home is termed invasion. Since this process usually involves competition, it will be considered last.

COMPETITION

Properly speaking, the struggle for existence in the plant world is between each plant and its habitat, the latter being changed by competition in consequence of the demands made upon it by other plants. An exception to the rule is the case of host and parasite. Between host and parasite there is a struggle not very different from that between two animals. Competition always occurs where two or more plants make demands for light, nutrients, or water in excess of the supply. If there is enough of any one of these factors, such as water in a swamp, there is no competition for that factor. Competition is a universal characteristic of all plant communities and is absent only in the initial stages of succession where the pioneers are still far apart. It increases with the increase in population in successive stages and continues to exist when the vegetation is stabilized.

Competition is essentially a decrease in the amount of water, nutrients, or light available for each individual. It is consequently greatest between individuals or species which make similar demands upon the same supply at the same time, *e.g.* between a group of even-aged clover plants as compared with a mixture of clover and timothy. Conversely, among plants that are absorbing at different levels and receiving light at different heights, competition is greatly reduced. In a few cases only is there actually competition for room. Such may occur in thickly grown crops such as radishes, but it seems never to occur under natural conditions, although rarely one root may grow through another instead of around it. The crowding of the swelling roots is, however, only an incident in the competition for water. There is no experimental proof of mechanical competition between roots or rhizomes in the soil, and no

evidence that their relation is due to anything other than competition for the usual soil factors—water, air, and nutrients. No matter how fully a soil seems occupied with underground parts, examination shows that there is usually room for more.

Competition and Dominance.—Properly speaking, competition exists only when plants meet each other on more or less equal terms. There is no competition between a host plant and the parasite upon it, but two or more parasites upon the same host may compete with each other. Parasite competes with parasite and host with host, though a rust, for example, may often be a decisive factor between two wheat plants. Neither does a dominant compete with a secondary herb of the forest floor, *e.g.* an oak with Jack-in-the-pulpit. The latter has adapted itself to the conditions made by the trees and is in no sense a competitor of the oak. Indeed, as in many shade plants, it may be a beneficiary and quite unable to grow in the area except for shade, humus, etc., afforded by the oaks. The case is different, however, when the seedlings of the tree find themselves alongside of the herbs drawing upon the same supply of water and light. They meet upon more or less equal terms and the process is essentially similar to the competition between seedlings alone on the one hand or herbs on the other. The immediate outcome will be determined by the nature of their roots and shoots and not by the dominance of the species. Naturally, it is not at all rare that the seedling tree succumbs. When it persists, it gains an increasing advantage each succeeding year and the time comes when competition between tree and herb is replaced by dominance and subordination.

The sequence of competition followed by dominance is repeated in every bare area, *e.g.* seedlings of one group—herbs, shrubs, trees—competing with those of another, and in each stage of the sere which develops upon it. The distinction between competition and dominance is well illustrated by the development of a secondary forest in a cut-over area or burn. All the individuals compete with each other at first, at least in so far as they occur in groups. With the growth of the shrubs they become dominant over the herbs and are, in turn, dominated by the trees. Herb still competes with herb and shrub with shrub, as well as with younger individuals of the next higher layer. Within the dominant tree layer, individuals compete with individuals and plants of one species with those of another. Thus, the rule, plants with similar demands compete when in the same area, while those with dissimilar demands show the relation of dominance and subordination. In a few cases, however, plants may be densely crowded and not compete with each other. This is illustrated by duckweeds (*Lemnaceæ*) which often completely cover the surface of ponds and streams. The tiny fronds are on an equality with respect to light, and the water supply is far in excess of the demands.

Nature and Effects of Competition.—The importance of competition both in the development of natural vegetation and in crop production is so great that it has received careful study.[99] When a group of seedlings, especially of the same species, are closely spaced, competition begins almost immediately. In the sunflower, for example, the first leaves of adjacent plants unfold simultaneously. The plants may be so nearly of the same height that the difference is only a millimeter. Yet this may be decisive, since one leaf overlaps the other. It continues to receive light and make photosynthate, while the shaded one can not. A difference of 2 or 3 days with full or reduced photosynthetic activity is quickly shown in difference in growth. The second pair of leaves of the fully lighted plant develops earlier, the stem is thicker and can better transport food to the rapidly growing roots. These, because of their greater food supply, penetrate a little deeper, spread farther laterally, and have a few more branches than those of their competitor. The increase in leaf surface not only reduces the amount of light for the plant beneath it, but it also renders necessary the absorption of more water and nutrient salts and correspondingly decreases the amount available. New soil areas are drawn upon for water and nutrients, and the less vigorous competitor must absorb in the area already occupied. The result is that the successful individual prospers more and more and becomes dominant. The other loses ground in the same degree and it must get along with what is left. If this is too little to support life, it succumbs; in any case, its development is increasingly retarded.

Effect of Competition upon the Growth and Functions of Plants.—Select 150 seeds of sunflower that are fairly uniform in size and soak them for 8 hours in tap water. Fill five containers of a capacity of at least 1 cubic foot with soil slightly drier than that in good tilth. Plant 4 seeds in one container, 16 in each of two others, and 50 in each of the two remaining containers. Soon after their appearance aboveground, thin the plants to 2, 8, and 32 per container, respectively, and in such a manner that all those in any container will be approximately equal distances apart. In the 2's and one series of 8's and 32's, keep the soil at a good water content so that competition will be for light only. In the second series, give the 8's and 32's only the same amount of water supplied to the 2's, regardless of the needs of the former, so that they will show competition for both light and water.

From week to week make careful observations on the growth of the plants. How soon does competition for light begin among the 8's? the 32's? By means of stakes and strings, prevent the plants from leaning far out. When the leaves greatly overlap, sketch, after noon on a sunny day, a leaf that is in part closely covered by another. Extract the chlorophyll and make a test for starch. When the 8's of the dry series are slightly flaccid and the 32's show wilting even in early morning, select after noonday a leaf of equal age (*i.e.*, fourth or fifth pair) from each of the three containers and make a test for starch. Also by direct observation in bright sunlight with the leaves still attached to the plants, determine the degree of opening of the stomata. By means of the cobalt-chloride method, determine likewise the relative rate of transpiration.[318] Determine the light values under the plants of each of the 5 containers.

When the 2's have reached a height of 18 to 24 inches, cut the plants at the ground line, wrap in moist paper to prevent wilting, and secure the following data from each

set, determining the average number in every case and arranging the results in the form of a table: height, diameter of stems above cotyledons, number of leaves, length and width of largest leaf, average leaf area of a few representative plants from each container, and dry weight. In a second table, using the 2's as 100 per cent, show the percentage reduction in leaf area and dry weight of the 8's and 32's under each of the two degrees of competition.

Competition within the Species.—The simplest case of competition is among plants belonging to the same species. At first, differences in height, leaf expanse, penetration, and spread of lateral roots are very slight. But as a result of competition there is great variation in all of these characters as well as in the ability to produce fruits and seeds. This is particularly true of annuals and perennials belonging to the same generation. Unlike plants of different species and requirements,

FIG. 82.—Representative sunflowers from the competition plots on July 2. The one on the right is from the 2-inch and that on the left from the 32-inch spacing.

their needs are so similar that they can not readily adjust themselves to the presence of others.

The course of competition among such plants is well illustrated by the following experiment: Cultivated sunflowers were grown in six large field plots under very uniform condition of soil, etc. The seeds were planted 2, 4, 8, 16, 32, and 64 inches apart, one rate of seeding in each plot. Competition among the 2-inch plants began soon after germination. Owing to elongation, these plants soon became tallest. Very soon, competition for light began among the 4's. Since each plant received more light and consequently could make more food than the 2's, they outstripped the latter but were, a little later, exceeded in height by the 8's. Thus, as the season progressed, each group in turn had for a time the tallest plants (Fig. 82). The 64's were so widely spaced that little or no competition occurred and they developed normally. The

average development of the mature plants in each plot is shown in Fig. 83. The correlation between growth of tops and roots is evident. The 2's, excluding suppressed plants which died, had an average height of 3.3

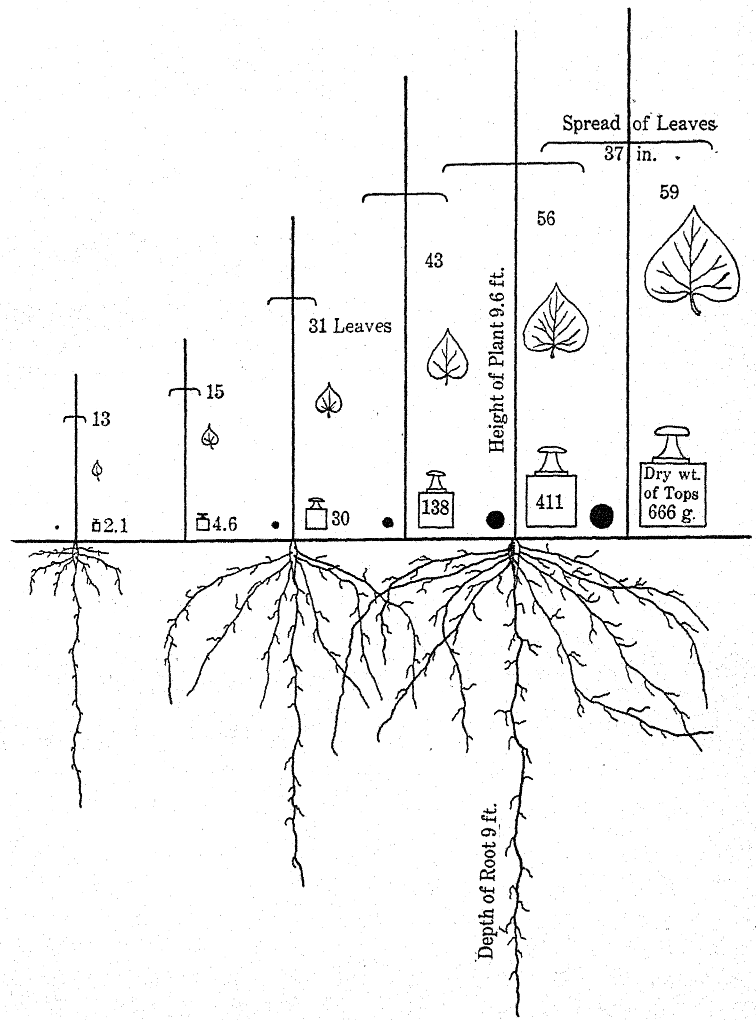

FIG. 83.—Diagram showing the relative development of mature sunflowers grown 2, 4, 8, 16, 32, and 64 inches apart, respectively, in field plots. The height varied from 3.3 to 10 feet, the diameter of stems from 5.7 to 47 millimeters. The relative leaf surface is shown in Fig. 84. The spread of leaves, *i.e.* diameter of the plant, ranged from 5 to 37 inches.

feet and a root depth of 5 feet; the 32's were 9.6 feet tall and 9 feet deep. The small transpiring and food-making surface of the 2's (24 square inches) is in accord with the shallow penetration and slight spread of the lateral roots. The great leaf surface of the 32's (3,426 square inches) was

supplied with water and nutrients by a network of roots that extended deeply and four times as widely (Fig. 84).

Repeated soil sampling showed that, in general, water content was lowest in the thicker plantings and more abundant in the thinner ones. Often, however, one of the vigorous, widely spaced plants was using as much water as the 16 or 256 smaller ones occupying a similar area. Each of the latter was not only deprived of sufficient water, having to share it with its competitors, but also its pale-yellowish, sickly color clearly indicated, what sampling confirmed, a lack of sufficient nitrogen. Competition for light was, moreover, severe. In midsummer, for example, the light received by the lowest green leaves was 12, 24, 31, 33, 40, and 80 per cent of full sunlight, respectively, from thicker to thinner plantings. Hence, not only was photosynthetic activity greatly reduced in the denser plantings, but also dead leaves and completely suppressed plants were numerous.

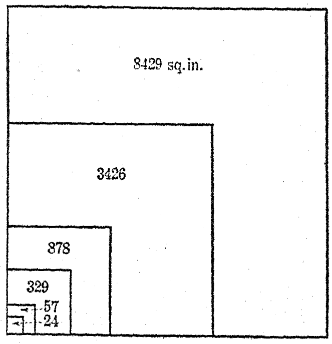

FIG. 84.—Relative leaf surface of sunflowers grown at distances of 2 to 64 inches apart in the field.

The poor conditions for growth were clearly reflected in the production of heads (Fig. 85). Only a few of the dominant plants among the 2's

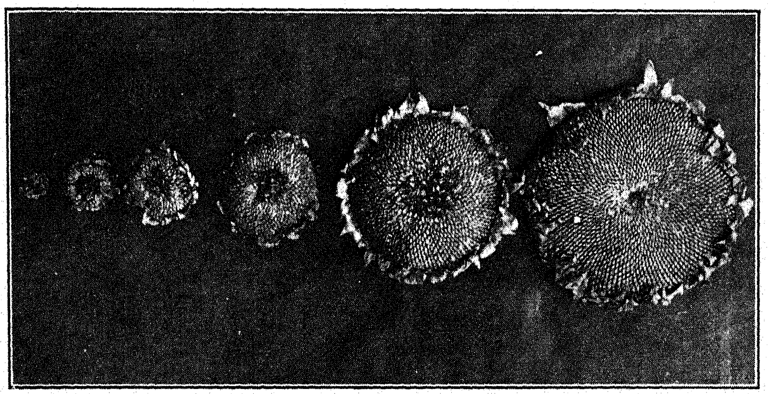

FIG. 85.—Heads of sunflowers grown at distances of 2 to 64 inches apart in the field. The largest is 8 inches in diameter.

bore seeds. These averaged only 15 per head as compared with 507 among the 16's and 1,803 among the 64's. The seeds, moreover, were very poor. In groups of 100, the relative weights were 0.9, 3.0, and 5.9 grams, respectively. Since repeated experiments on a wide range of annual plants have shown that heavy seeds give the greatest germination,

most vigorous plants, and largest yields, the chances of reproduction by greatly suppressed plants are clearly decreased.[49,599]

Under natural conditions of chance distribution, the development of plants is closely correlated with the degree of competition. This is illustrated in Table 2 where the number, height, and diameter of great ragweeds (*Ambrosia trifida*) were determined in a small, waste area on a flood plain.

TABLE 2.—DEVELOPMENT OF RAGWEEDS IN RELATION TO DEGREE OF COMPETITION

Number of plants per square meter	Average height, feet	Average diameter of stem, millimeters
12	11.3	19.0
20	10.6	13.0
33	9.3	9.9
64	8.4	7.4
73	7.8	7.2
84	6.8	6.2
154	5.0	3.4

Competition among monocotyledons is very similar, except that in grasses the number of stalks is increased by tillering. Where Marquis spring wheat was grown at half the normal rate, normal, twice normal, and four times normal, differences were soon apparent. The thickly sown plants, because of competition for light, grew erect, while the thinly planted ones tillered and spread widely. The spindling, yellowish, nitrogen-starved, crowded plants contrasted strikingly with the deep green, shorter ones which were more widely spreading. The number of tillers decreased from four to one. The gradation in number and height of stems and number and size of leaves in older plants is shown in Fig. 86. The plants in the thinner plantings had more water, more nutrients, and a root system better developed for absorption. The larger plants, for example, had an average of 37 main roots, the smaller ones only 9. They also received more light, the range being 80, 58, 37, and 24 per cent of full sunlight, respectively, in the different plantings. The leaf area per plant ranged from 92.6 to only 6.9 square inches. At the time of harvest, the thickest planting averaged only 1 head per plant, there being 2 in the normal planting and 4 in the half normal. Moreover, as shown in Fig. 87, there was a marked difference in the size of heads. The yield from 1,000 heads under the several degrees of competition varied inversely with the severity of competition. The yield per acre was almost as great in the thinnest planting (19 bushels) as in the normal (21 bushels). Owing to the great increase in the number of plants, the yield was slightly

larger in the twice-normal planting (23.7 bushels) but fell to 21.6 bushels in the four normal.[99]

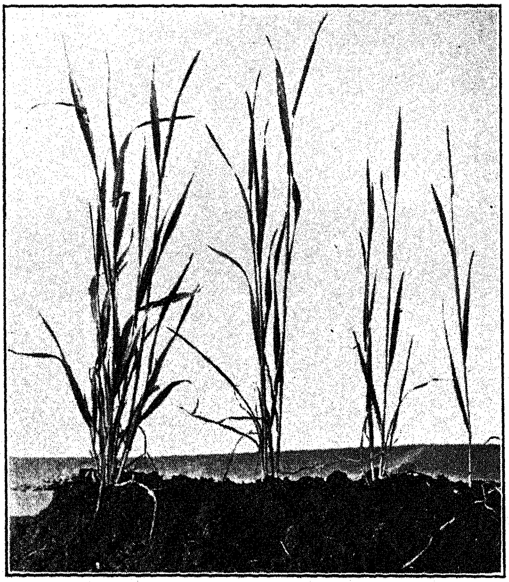

FIG. 86.—Representative plants of Marquis spring wheat from four plots with different rates of planting. The plant on the left is from the thinnest planting.

FIG. 87.—Heads of wheat of average size from plots with different rates of planting. The one on the right is from the thickest planting.

Much work has been done to determine the best spacing of cotton and other crop plants to obtain the highest yields.[355] In general, the

results are similar to those obtained for wheat. Among coniferous trees, crowding in forest stands reduces the quantity of seed produced in proportion to the density of the stand.[244]

Competition between Different Species.—Competition is closer between species of like form, such as grass with grass, than between those that are dissimilar, such as grass with dicotyledon. Shrub competes sharply with shrub, and tree with tree, the outcome being a reduction in the number or size of the individuals or the total disappearance of one or more species. The characters of the root, stem, and leaf ordinarily determine the outcome. The greater the difference between species in one or all of these characters the less severe the competition. A deep taproot system such as that of the wild rose competes but slightly or not at all with a shallow-rooted grass. Neither does the taller rose receive light at the same level as the grass. Hence, the two may grow together with scarcely any competition except in the seedling stage.

In closed, stabilized communities in grassland, competition for water is so severe that the growth of all species is reduced. Often, they are unable to produce seed, especially during years of drought, and normally the inflorescence and number and size of seed are reduced. Water is the controlling factor, as may be shown by removing all the plants from a quadrat except the species under observation. The removal of competing plants results in an increase of water which causes a marked increase in growth. Figure 26 illustrates typical differences in growth during a single season. In the case of *Helianthus rigidus*, growth in height increased 28 per cent and the diameter of the stem was doubled. The leaves were three times as broad, the heads twice as numerous and 35 per cent larger, and there were more and larger seeds. Where all but the central 10 square decimeters of vegetation were removed from other quadrats and the sod overturned, the yield in these central areas was increased two-thirds and, in some instances, almost doubled.

Light plays an important rôle in competition even in grassland, as has been fully demonstrated. Mixed cultures of various grasses and of grasses and dicotyledons have been studied in detail. Among the former, even in early summer of the first season's growth, the light intensity is reduced to 10 per cent or less. Hundreds of seedlings succumb and even the dominants may tiller only poorly. Seedling grasses, like seedling trees, often endure much shading. Figure 88 shows the development of a competition culture of tall panic grass (*Panicum virgatum*) and evening primrose (*Œnothera biennis*). Œnothera, being slightly taller and extending its roots deeper than those of the grass, soon gained the lead. The low light intensity, about 30 per cent, was shown by the attenuated grasses and the yellowish color of the lower leaves. In late summer, the light values were only 18 per cent at a height of 3 inches. By fall, 25 per cent of the grasses had died and over half of the remainder

were suppressed. Only a few of the grass leaves overtopped the competitor and received full sunlight. These were making photosynthate almost twice as rapidly as the shaded leaves of the suppressed plants. By the end of the second season, the biennial Œnothera had completed flower-stalk production, seeded, and died. It failed to reproduce in

FIG. 88.—*A*. Competition between tall panic grass and evening primrose. There are 264 grass seedlings and 48 of evening primrose in the central 100 square inches. *B*. The same culture 20 days later. The number of evening primroses is the same but there are 55 more grass seedlings.

the area the following spring. The few starved grasses that remained, in the absence of their competitor, made a renewed growth. They tillered abundantly and soon had complete and permanent possession of the area.

Prairie species show a great range in their ability to endure shading. The lower leaves of some, *e.g.* prairie false boneset (*Kuhnia glutinosa*), will turn yellow and die when light is greatly reduced; others, like blazing

star (*Liatris*), make a slow growth when the light values are only 5 to 10 per cent and may appear above the general grass level only after a period of several years. A dominant must have several characteristics. Among these are size—usually it has a stature as great as or greater than its competitors—abundance, and duration. It must occur in sufficient numbers so that it controls the area and be of long duration so that it can hold it against invaders.

Competition among Cultivated Crops.—Man's chief concern in growing plants is to secure the largest and best yields. One of his main problems, although usually not recognized as such, is to regulate the degree and kind of competition. Aside from the preparation of a good seed bed to promote rapid and uniform germination and establishment, and the maintenance of soil fertility, his chief efforts are directed toward tillage. Extensive experimental evidence shows that among both field and garden crops the chief value of tillage lies in weed control (*i.e.* competition) and not in the preservation of a soil mulch.[79,527] Most cultivated plants have been so long aided by man that they no longer successfully compete with weeds. If the latter are not controlled, the growth and yield of the crop are greatly reduced. In Illinois, for example, corn averaged 46 bushels per acre where weeds were kept down by scraping the soil surface but only 7 bushels where the weeds were allowed to grow.[360] Where the weeds have been eradicated or are insignificant, however, further cultivation is of little or no value, and if it is so deep as to cause root injury it may be distinctly harmful.

In well-kept fields, competition is between individuals of the particular crop. This increases with thickness of planting upon soils of equal fertility and water content. Since more widely spaced plants develop larger individuals and fruits, the reduction in yield is not proportional to the reduction in stand. It has already been seen that wheat sown at one-half the normal rate produces a yield nearly as great as that sown at the normal or even twice the normal rate. Where three grains of corn were planted per hill in hills 3.5 feet apart, and 7 per cent of the hills were missing, the yield was 86 bushels per acre. Where 13 per cent were missing, the yield increased to 88 bushels. A decrease of 17 per cent in the stand gave a yield of 84 bushels, and with a decrease of 57 per cent the yield was 57 bushels. In another experiment where three plants were grown per hill, the yield was 83 ears per 100 plants; two per hill yielded 96 ears; and one per hill, 168.[281] The yield of the two hills of potatoes adjacent to a space where the hill has been skipped may be 40 per cent more than that of two other competing hills.[313]

Frequently, greater yields are obtained by increasing the density of planting, but the size of both vegetative parts and fruits is reduced. This may be desirable as in such crops as carrots, beets, etc. Onion sets of small size are obtained by very close planting as is also the medium-

sized head of cabbage or cauliflower. The total yield of potatoes may be increased by planting thickly but the yield of the larger tubers is reduced.[57]

Variety and yield tests of corn and many other crops are usually made under the "ear-to-the-row" method of planting. The results of such tests have been shown to be often completely misleading because of the effects of competition. Where large and small varieties of corn, for example, were grown in alternating rows, the smaller variety yielded only 66 per cent as much as the larger one; and when planted in the same hill, only 47 per cent. The larger variety was 8 feet tall and had a leaf area more than twice as great as that of the smaller one which was less than 6 feet in height. Undoubtedly, the root system was proportionately more extensive. That the small variety was being robbed of light, water, and nutrients properly belonging to it was shown by yields where each crop was surrounded by its kind. In this case, the corn was grown in plots with five rows per plot, and only the three center rows were harvested. Thus, the so-called border effect, where the small variety was poorer and the larger one better, was eliminated. The yield of the small variety under these conditions was 85 per cent as great as that of the large one. Similarly, thin stands of wheat in rows alternating with thick ones yielded only 68 per cent as much as the thick. But the three middle rows in alternating five-row blocks of thin and thick stands yielded 90 per cent as much as the thick. Thus, it seems clear that any crop that is being tested should be surrounded by a crop of the same kind to eliminate the factor of unusual competition.[281]

In some periods in the development of a crop, competition may be distinctly beneficial. In most orchards, fertilizers evoke the greatest response when they are applied so that nitrogen is available early in spring. No cover crop should be competing with the trees for nitrogen at this time. A growth of sod often so reduces the supplies of water and nitrates that the size of fruit is greatly decreased and the yield much reduced. Oats sown in late summer, however, use a large amount of both water and nitrogen so that the growth of the trees is correspondingly checked. They ripen their wood and enter the winter properly prepared to withstand the cold. The mulch of oats, moreover, insulates against freezing of the soil and protects the tree roots which are more tender than the tops. It holds the fallen leaves about which the snow accumulates. The cover crop is plowed under in the spring and thus manure is added at a time when it is most needed.[44]

Evaluation of the Several Factors.—The effects of the several factors for which plants ordinarily compete, *viz.* water, light, and nutrients, are almost always so integrated that they can be determined only under controlled conditions where all but one are eliminated.

To Evaluate the Relative Effect of Water and Light in Plant Competition.—Secure two cylindrical containers 4 inches in diameter and 8 to 12 inches deep. Place

each in the center of larger ones, at least 12 inches in diameter and depth, so that the tops of the two are at the same height. Fill both large and small containers with well-compacted potting soil. Fill two similar larger containers in like manner. Plant 12 sunflower seeds in each, spacing them regularly 2 inches from the edge of the large containers. Cover with a thin gravel mulch, and later thin to 10 per container.

When the plants begin to produce the third pair of true leaves, plant a second crop of sunflowers, 6 per container (later to be thinned to 3) in the central area, *i.e.* in the cylinders in two cases. At the same time, fasten a stout string about the base of one container with a cylinder and one without. Bend the first crop of plants over the edges of the containers and tie them down in such a way that they will cast no shade on the second crop. Thus, four conditions of competition are provided, *viz.* (1) no competition, (2) competition for water only, (3) competition for light only, and (4) competition for both water and light. Water all of the plants sufficiently to keep the first crop from wilting (but do not add an excess), and also keep the soil in the central cylinders well moistened. Measure the light intensity above the seedlings under the first crop. It may be necessary to support the weaker seedlings by means of tying them to wires thrust into the soil.

When the seedlings without competition are beginning to develop the third pair of leaves, and before the deterioration of the lower leaves of the first crop permits the entry of too much light, cut the plants at the ground line and secure the following data, which should be arranged in a table showing increasing effects of competition: height, diameter of stem above cotyledons, number of leaves, leaf area exclusive of cotyledons, and dry weight. Also determine the relative root depth in the two cylinders.

In a series of experiments, large containers, 1 square foot in cross-section, were filled with 2 cubic feet of fertile soil. Plants were grown in series, sunflowers and cockleburs (*Xanthium commune*) in different containers at the rate of 2, 4, 8, 16, and 32 per container, and wheat at the rate of 4, 8, 16, 32, and 64 plants. At the time of planting, the soil, which was of equal weight in each can, had an optimum water content. Water loss from the surface was prevented by a thick gravel mulch (Fig. 89). Transpiration was determined by repeated weighings, and both water and a complete nutrient solution added as required in the control series. In the competition-for-water series, at every weighing each container received only the amount of water necessary to restore the original weight of the container with the smallest number of plants. Thus, competition for water became more and more severe as the number of plants per culture increased. Nutrients were maintained in some series by adding a nutrient solution in amounts proportional to the increasing density. In all but the thinnest cultures, there was also competition for light.

Where eight wheat plants were grown per container with both water and nutrients maintained, the dry weight per plant was 4.5 grams; where they competed for nutrients, only 4.4 grams, but where they competed for water, it was only 3.7 grams. Leaf areas in the same sequence were 35, 36, and 25 square inches. Denser cultures gave similar results

(Table 3). A progressive decrease in amount of growth also occurred even where competition was for light only.

TABLE 3.—DEVELOPMENT OF MARQUIS SPRING WHEAT UNDER DIFFERENT CONDITIONS OF COMPETITION

(Average dry weight per plant in grams, leaf areas, in parenthesis, in square inches)

Competition for	8's	16's	32's	64's
Water and light	3.7 (25.1)	2.0 (9.0)	1.2 (4.0)	0.7 (2.8)
Nutrients and light	4.4 (36.3)	2.2 (12.0)	1.8 (9.8)	1.0 (3.7)
Light only	4.5 (34.6)	2.6 (11.6)	1.7 (7.8)	1.0 (3.1)

In the case of cockleburs, where eight plants were grown per container, the average dry weight per plant when competing for water was 2.7 grams; for nutrients, 3.6 grams, which was fully as good as the control.

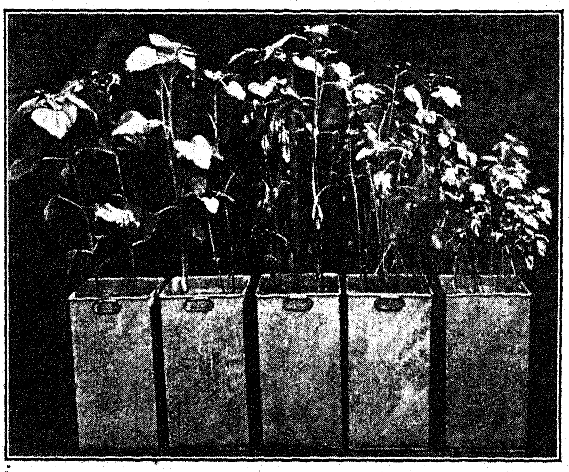

FIG. 89.—Sunflowers competing for light and water. All are of the same age, but the 4's, 8's, 16's, and 32's received only as much water as the 2's.

Where they were shaded so as to receive no more light than that of a culture four times as dense, the dry weight was reduced to 2.1 grams. Leaf areas in the same sequence were 64, 79, and 45 square inches. When competing for both water and nutrients, the dry weight was greater than in competition for water alone. This is the usual sequence and illustrates the fact that a water supply that becomes deficient later in a rich soil is much more harmful to plants (which start growth luxuriantly) than in a less fertile soil.

Rôle of Competition in Succession.—Competition exerts a controlling influence in succession. Among pioneers in a bare area, except in the hydrosere, it is usually restricted to the soil, where the roots compete with each other for water. As vegetation develops, competition for

light plays an important part and the regular outcome, in many cases, is dominance. This is particularly true as the bare area becomes covered and success in ecesis comes to depend upon the ability to overshadow other plants. The taller plant gradually gains the upper hand, partly because it receives more light and makes more growth and partly because its demands are increased by greater transpiration. In order to meet this demand for a greater water supply, the root system develops more extensively and encroaches upon areas occupied by smaller plants. At the same time, the shorter plant receives less light and transpires less and its needs for water diminish. This interplay of competition and reaction occurs in all communities with individuals of different height and extent, but in varying degrees. It is well illustrated in the different types of grassland. Short grasses, like buffalo and grama grasses, arenot abundant in tall-grass prairie because of unsuccessful competition for light. In short-grass plains, tall grasses are usually absent because of their unsuccessful competition for water. In mixed prairie, there is enough water for a partial tall-grass cover and enough light for the understory of short grasses to thrive.

Where dicotyledonous herbs are abundant, competition for light is more severe. Thus, in grassland, as well as in forest, layers come to be developed although not with the same definiteness. *Antennaria*, certain species of *Astragalus*, and other prostrate plants form the lower or ground layer. The layer of grasses above is overtopped by one of dicotyledonous herbs such as goldenrods, asters, sunflowers, etc. The dominance of trees is only the outcome of a competition in which position means the control of light and, thus, of water. Where the water supply is in excess, as in submerged plants, competition of shoots alone may occur.

Competition, in affecting the supply of water and light, is most decisive during the development of the seedling and at the time of reproduction, particularly in the case of perennials and woody plants. Accordingly, it plays a large part in determining the number of occupants and of invaders in an area in each stage of a sere and thus in helping to control the course of development.

The general effect of competition between one group of plants and the invaders in each stage of the sere has already been sketched under succession. Those invading species that show the greatest resemblance to the occupants in the form of leaf, stem, and root experience the greatest difficulty in establishing themselves. Invasion of shrubs by shrubs, *Phragmites* by *Typha*, etc., is very difficult. On the contrary, species of unlike life-form enter either at a clear advantage or disadvantage, *e.g.* shrubs into grassland or herbs into forest. A reaction sufficient to bring about the disappearance of one stage can be produced only by the entrance of invaders so different in form or nature that they change the impress of the community materially or entirely. Vegetation becomes stabilized

when the entrance of such invaders is no longer possible. For example, while species of many vegetation-forms may enter a forest, none of them is able to place the trees at a disadvantage. Hence, the final forest stage, though it may change in composition, can not be displaced by another.

INVASION

Invasion is the movement of one or more plants from one area into another and their establishment in the latter. It is thus the complete and complex process of which migration, ecesis, and competition are the essential parts. It is going on at all times and in all directions. Invasions may occur in bare areas or in areas already occupied by plants.

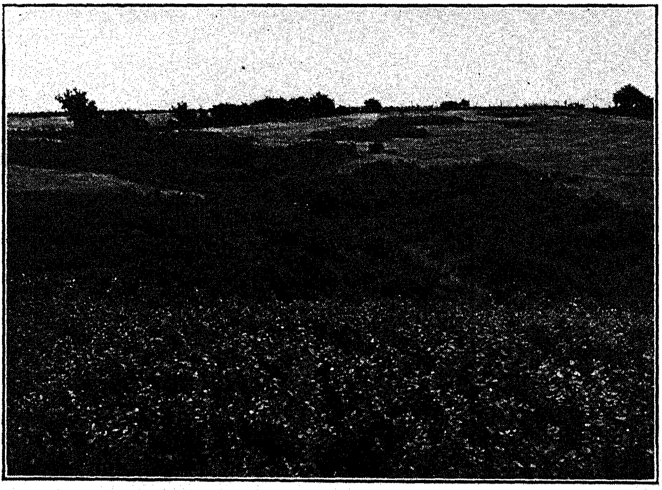

FIG. 90.—Coralberry (*Symphoricarpos*) invading grassland in eastern Nebraska.

The former initiates succession, the latter continues the sere by producing successive stages until the climax is reached. But even then invasion does not necessarily cease. As a rule, however, invasion into a climax community is either ineffective or it results merely in the adoption of the invader into the dominant population. Practically all invasions of consequence either populate bare areas or produce new developmental stages.

Effective invasion is nearly always local. It is usually mass invasion such as shrubs into grassland or willows on to sand bars (Fig. 90). It operates between bare areas and adjacent communities which contain species capable of pioneering and between contiguous communities which offer somewhat similar habitat conditions or at least contain species of a wide range of adjustment. Invasion into remote areas rarely has any successional effect, as the invaders are too few to make headway against the plants in possession or against those much nearer a new area.

The invasions resulting from the advance and retreat of the ice during glacial times were essentially local. They spread over large areas and moved long distances only as a consequence of the advance or withdrawal of the ice. The actual invasion at any one time was strictly local.

Invasion into a new area or plant community begins with migration and is followed by aggregation and competition, with increasing reaction. In an area already occupied by plants, ecesis is immediately followed by competition and reactions, *e.g.* decrease of light and water is quickly produced. Throughout the whole process of the development of vegetation, migrants are entering and leaving, and the interactions of the various processes come to be complex in the highest degree.

Kinds of Invasion.—Local invasion in force is essentially *continuous* or *recurrent*. Willows or cottonwoods, for example, may invade the new deposits made by a river only to be destroyed by unusual floods. But by invading the area each year or after each catastrophe, these deposits may finally be built up and covered with a willow-cottonwood forest. Likewise, trees might invade grassland only to be repeatedly burned with the grasses. By continuous or recurrent invasion, conditions may finally arise where the grasses disappear as the result of shading and prairie fires will cease. Between contiguous communities, invasion is *mutual*, that is, it takes place in both directions, unless the communities are too dissimilar. There is an annual movement from each community into the other, and often a forward movement through each, resulting from the invaders of the previous year. By far the greater amount of invasion into existing vegetation is of this sort. The result is a transitional area or ecotone between the two communities, *e.g.* shrub-herb area between woodland and grassland, water lily-bulrush area between floating plants and reed swamp. Such ecotones indicate the next stage in development. The movement into a bare area is likewise continuous, though not mutual, and, hence, there is no ecotone during the earlier stages. In continuous invasion, an outpost, such as trees or shrubs in grassland, may be continuously reinforced, permitting rapid aggregation and ecesis and the production of new centers from which the species may be extended over a wide area.

Intermittent invasion commonly arises through intermittent or periodic movements into distant regions. Such invasion is relatively infrequent but is often striking, owing to the fact that the invader often wanders far from the original home. It is rarely of consequence in causing succession. Invasion is *complete* when the movement of invaders into a community is so great that the original occupants are driven out. This is characteristic of the major stages of succession where one life-form replaces another. Where the number of individuals is sufficiently small to be adopted into the community without changing it materially, invasion is said to be *partial*. Partial invasion is more frequent though less

conspicuous than complete invasion. Between the two there are necessarily transitions. *Permanent invasion* occurs when a species becomes permanently established in a more or less stable community. The term is entirely relative. Spike rush, for example, illustrates permanent invasion into a sedge meadow. But in each sere, initial and medial stages are temporary in comparison with the climax. Though the initial stages of a rock sere may last for centuries, they must finally pass in the course of development just as the climax stage will disappear should there occur a marked change in climate.[115]

Manner of Invasion.—Bare areas present very different conditions for invaders from those found in plant communities. This is due to the absence of competition and often to the reactions the plants have exerted upon the habitat. Conditions for germination are nearly always more favorable in plant communities, but the fate of the seedling and adult is then largely determined by competition. Open communities are invaded readily, closed ones with more difficulty if at all. Open communities are those which have factors in excess of the demands of the existing populations; in closed ones, the plants are in close adjustment with the usual supply. A community, therefore, is not necessarily open (desert, spruce forest) because a part of the surface is bare. Secondary bare areas usually afford maximum opportunity for invasion. This is partly due to lack of competition but especially to the fact that conditions are more or less optimum for the germination and growth of a wide range of species. Primary areas (water, rock, sand) present only extremes of water content, and thus exclude all invaders except a few pioneers.

In all invasions, after the first or pioneer stage, the relative level of occupants and invaders is critical. Invasion may occur at three different levels. A community may be invaded at its level, *i.e.* by species of the same general height as those in occupation, or below or above this level. When invasion is at the same height, *e.g.* trees in forest, the level has no effect and the sequence of development is determined by other features such as ability of seedlings to endure shade. If it is above the level of the occupants, such as mosses above crustose lichens, the newcomers become dominant as they stretch above their neighbors and soon give character to a new stage. This is notably the case with shrubs and trees in which the close dependence of the sequence of stages upon life-form is most evident. When invasion is below the existing level, it has no direct influence upon the dominant species unless the latter are handicapped as in overgrazed mixed prairie. Such invaders normally take a subordinate place as secondary components of the community. A unique exception is that of the peat moss, *Sphagnum*. In wet climates it may invade the forest floor where springs or seepage water occur. Holding the water like a sponge and annually increasing its territory, it may so water-log the area that the forest disappears.

To Determine the Water-retaining Power of Sphagnum.—Place loosely 100 grams of air-dry, commercial peat moss (*Sphagnum*) in a small sack of cheesecloth and submerge it in water for an hour or longer. Reweigh and determine the percentage of water retained, based on the dry weight of the moss. Examine a living leaf under the microscope and make out the narrow, elongated, living cells containing chloroplasts and the intervening, larger, colorless dead cells. The latter are held open by spiral thickenings on the inner surface of the cell walls and air escapes through the pores as water enters the cell. Also, view the leaf in cross-section.

Barriers.—Any feature of the topography or any physical or biological agency that restricts or prevents invasion is a barrier. It may be a mountain range, a highly alkaline soil, or grazing animals. Topographic features are usually permanent and produce permanent barriers. Biological ones, *e.g.* cultivation and burning, are often temporary and exist for a few years or even a single season. Temporary barriers are often recurrent, however. Barriers are complete or incomplete with respect to the thoroughness of their action. A water-filled depression permits certain plants to ecize, but a large lake is a complete barrier to most land plants, since they can neither migrate across it nor ecize in it. The chief effect of barriers upon invasion is exerted upon ecesis and not upon migration.

Physical Barriers.—Barriers are physical when due to some marked topographic feature such as an ocean, lake, river, mountain range, or desert. All of these affect invasion because of their dominant physical factors, *i.e.* excess or deficiency of water, temperature, nutrients, etc. They prevent the ecesis of species coming from very different habitats, though they may, at the same time, serve as conductors of plants between similar habitats, as in the case of a river between two lakes. A body of water is a barrier to mesophytes and xerophytes; deserts set a limit to the invasion of mesic and hydric plants, while they favor xeric ones. By its reduction of temperature, a high mountain range restricts the extension of plants of lowlands and plains. It is also more of an obstacle to migration than most physical barriers, because of difficulty of movement up its slopes. Any bare area with extreme conditions is a barrier to the invasion of adjacent communities. It is not a barrier to the development of a sere upon it, since the proper pioneers are always able to invade.

Biological Barriers.—Biological barriers comprise plant communities, man and animals, and parasitic plants. Invasion is limited by a plant community in two ways. An association, *e.g.* woodland, acts as a barrier to the ecesis of species invading it from associations of another type on account of the physical differences of the habitats. Whether such a barrier be complete or partial will depend upon the relative unlikeness of the two areas. Shade plants are unable to invade a prairie, though the species of open thickets or well-lighted woodland may do so to a certain degree. A mature forest, on account of its diffuse light, is a

barrier to sun-loving plants, while a swamp, because of its excess of water and poor aeration sets a limit to the invasion of species of both woodland and grassland. Forests and thickets act as a mechanical obstacle especially to the migration of tumbleweeds and many other wind-distributed plants. Closed communities whether forest, grassland, or desert, exert a marked influence in decreasing invasion by reason of the intense and successful competition all invaders must meet. Closed associations usually act as complete barriers, while more open ones restrict invasion in direct proportion to the degree of occupation. Thus, the number of stages in succession is determined largely by the increasing difficulty of invasion as the area becomes stabilized.

Man and animals affect invasion by the destruction of disseminules. Both in bare areas and in seral stages, the action of rodents and birds is often decisive to the extent of altering the whole course of development. Man and animals act as barriers by flooding, draining, etc., or, when they turn the scale in competition, by cultivation, grazing, trampling, parasitism, or in other ways.

The absence of pollinating insects is sometimes a curious barrier to the complete ecesis of species far out of their usual habitat or range. When red clover was first introduced into New Zealand it was unsuccessful as a crop, since it did not produce seed. With the introduction of the bumblebee, upon which the plant is usually dependent for pollination, the clover became a very successful invader.[528] Similarly, Smyrna figs when introduced into California grew well and blossomed but did not set fruit. Their ecesis was incomplete until the small wasp which effects pollination was also introduced. Parasitic fungi decrease migration in so far as they destroy seeds or reduce the number produced. They restrict or prevent ecesis either by the destruction of invaders or by placing them at a disadvantage with respect to the occupants.

Changes in Barriers.—A closed formation, such as a forest or meadow which acts as a decided barrier to invasion, may disappear completely as the result of a landslide, flood, or burn, or through the activity of man, and leave an area into which migrants crowd from every direction. A marsh or swamp ceases to be a barrier to prairie xerophytes during a period of unusually dry years, such as regularly occurs in semiarid regions. Conversely, during a series of wet years mesophytes may enter into the development of a sere at a stage where they are usually barred by deficient water content. The succession may be much shortened and one or more stages omitted. Many xeric habitats such as dunes, gravel slides, blow-outs, prairies, etc., are barriers during summer and autumn but not during spring when the dry, hot surface becomes sufficiently moist to permit the germination and growth of invaders. The influence of distance as a barrier has been discussed under migration.

CHAPTER VIII

REACTION AND STABILIZATION

A plant or a community produces various effects upon the habitat. All such effects are termed reactions. These are not to be confused with the impress which the habitat makes upon the plant. A habitat offers a certain amount of the factors—water, light, nutrients, etc.—to growing plants and the vegetation adjusts and adapts itself to this supply. If water is not abundant, it takes on a xeric impress; if in excess, a hydric one. But in any case the plants react upon the habitat, changing one or more of its factors to a decisive or appreciable degree. Such changes, however, can not go on indefinitely. After many generations of plants have grown on an area and it has been occupied successively by the various stages of a sere, there finally appears a community of plants which is in complete adjustment with the habitat thus modified under the control of the particular climate, that is, stabilization is attained.

REACTIONS

The effects of habitat on plant and of plant on habitat are mutually complementary and often very complex. As a rule, there is a primary reaction accompanied by several or many secondary ones. Trees decrease light and by so doing they also modify temperature, humidity, and evaporation. Sometimes two or more factors are affected directly and critically, *e.g.* marsh grass greatly reduces both water content and light. Vegetation exerts its effect almost wholly on the physical factors.

The reaction of a community is usually more than the sum of the reactions of the component species and individuals. Although it is the individual plant that produces the reaction, the latter usually becomes recognizable through the reaction of the group. A community of trees casts less shade than the same number of isolated individuals, but the shade is constant and continuous and, hence, controlling. The leaf litter that forms the leaf mold and duff is only the total of the fallen leaves of all the individuals, but its formation is completely dependent upon the community. About isolated trees, it is blown away or dries in the sun and it rarely accumulates except where the trees are in groups. Widely scattered plants can scarcely accumulate wind-blown sand and hold it in dunes, or scattered floating ones cause much sediment to settle from silt-laden water.

Some reactions are the direct consequence of a functional response on the part of a plant. This is exemplified by the decrease of water by absorption, the increase of humidity as a consequence of transpiration, and the weathering of rock by the excretion of carbonic acid. Others are the immediate outcome of the form or habit of the plant body. For example, the successful reaction of pioneers in gravel-slides is produced almost wholly by mat, rosette, or bunch forms with extensive or deep-seated roots (Figs. 91 and 92). In a primary area, the reaction is exerted by each pioneer alone and is then augmented by the family or colony.

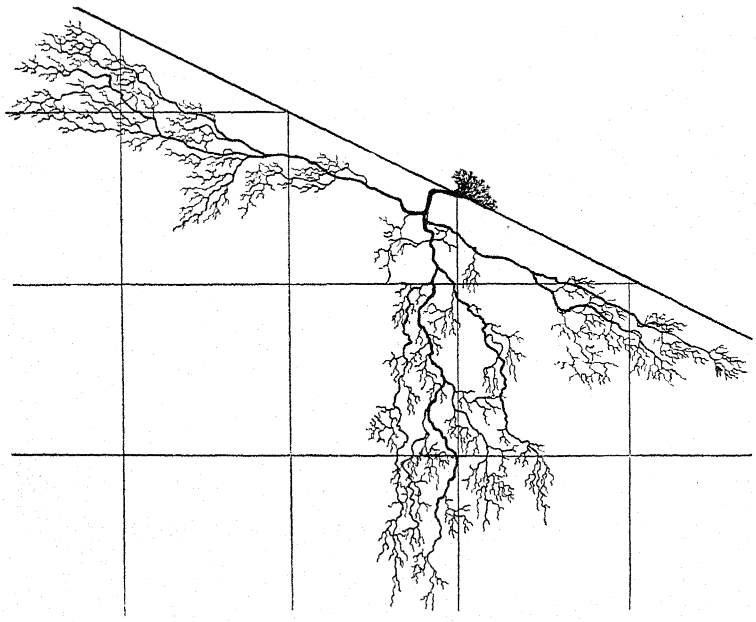

Fig. 91. A gravel-slide plant (*Paronychia jamesii*). Because of the extensive root system the gravelly soil within a radius of two or more feet of the plant is held more or less firmly in place. Compare Fig. 45.

It extends as the communities increase in size and comes to cover the whole area as vegetation becomes closed. Reactions are often felt for a considerable area around the individual or group, especially where exerted against the eroding action of wind or water or the slipping consequent upon gravity. In most secondary areas or seral stages, the reaction is the combined effect of the total population. But the preponderant rôle is played by successful competitors and particularly by the dominants. These determine the major or primary reactions, in which the part of the secondary species is slight or negligible.

Rôle in Succession.—In the development of a primary sere, reactions begin only after the ecesis of the first pioneers and are narrowly localized about them and the resulting families and colonies. They are largely

mechanical at first and consist in binding sand or gravel, producing finely weathered material, or building soil in water areas, etc. In secondary seres, extensive colonization often occurs during the first year and reaction may at once be set up throughout the entire area. The reactions of the pioneer stage may be unfavorable to the pioneers themselves, or they may merely produce conditions favorable for new invaders, which succeed gradually in the course of competition or become dominant and produce a new reaction unfavorable to the pioneers. Naturally, both causes may and do operate at the same time. The general procedure is essentially the same for each successive stage. Ultimately, however, the time comes when reactions are more favorable to occupants than to invaders, and the existing community becomes more or less permanent, constituting a climax or subclimax. In short, a climax vegetation is completely dominant, its reactions being such as to exclude all other species. In one sense, succession is only a series of progressive reactions by which communities are selected out in such a way that only that one survives which is in entire harmony with the climate. Reaction is thus the keynote to all succession, for it furnishes the explanation of the orderly progression by stages and the increasing stabilization which produces a climax.

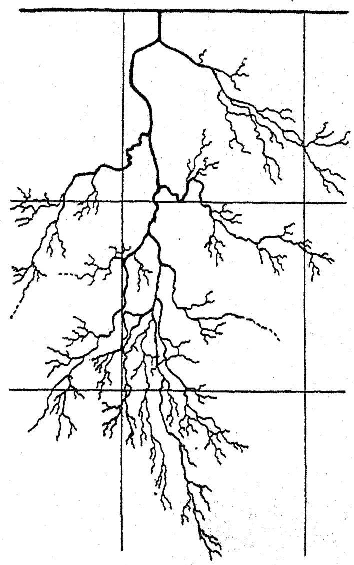

Fig. 92.—Surface view of a single root of *Paronychia jamesii* at a depth of 2 to 2.5 inches.

Kinds of Reactions.—There are two main groups of reactions in accordance with the place in which they occur, *viz.* soil reactions and air reactions. The soil as a fixed substratum is much more affected by plants and soil reactions are correspondingly much more numerous than those in the air. The former may be classified, in accordance with the factor directly affected, under (1) soil formation and structure, (2) water content, (3) solutes, and (4) soil organisms. Air reactions will be considered under (1) light, (2) other factors (humidity, temperature, etc.), (3) effect upon local climate, and (4) air organisms.

SOIL FORMATION

Plants may produce a new substratum or soil in four essentially different ways: (1) by the accumulation of the plant bodies themselves, usually under conditions which retard or prevent decay; (2) by the concretion of mineral matter into rock or marl through the activity of

water plants; (3) by the weathering of rock into fine soil by the excretion of acids and mechanical effects of roots; and (4) by the resistance which plant bodies offer to moving air and water, resulting in the deposition of particles in transport.

Reaction by Accumulating Plant Bodies or Parts.—The complete decomposition of plants in contact with air prevents any considerable heaping up of plant remains in ordinary habitats. Accumulation in quantity can occur only under water, where oxidation is largely or completely prevented. This reaction is brought about only by plants which grow in water or in wet places. The formation of soil may be hastened, however, by the incorporation of transported material, including ter-

FIG. 93.—Section of a peat deposit several feet in depth.

restrial plants as well as animal remains and detritus. This type of soil building is the characteristic reaction of aquatic and amphibious communities and occurs in both fresh and salt water. Peat may be formed from the remains of submerged algæ, cattails, etc., as well as from *Sphagnum*. In fact, the peat substratum is found universally wherever plants decompose in the presence of insufficient oxygen (Fig. 93). A similar process has occurred throughout geological history, resulting in the formation of coal at various times from the Paleozoic to the Tertiary.

In many boreal and mountain regions, *Sphagnum* usually enters during or near the close of the amphibious stage of the hydrosere and gives a new lease to accumulation under circumstances that may almost completely inhibit decomposition. The water of sphagnum bogs is notably free from organisms causing decay, largely due to very deficient

aeration. After a time, the moss layer becomes so thick that other plants may enter because of the decreasing water content of the surface, which controls development. Sphagnum may also extend as a floating mat over pools and ponds and eventually fill them with peat. Soils are sometimes produced from the deposition of diatom shells in marshes, etc., occasionally building up extensive meadows as in Yellowstone National Park. Relatively, they are of little importance.

Reaction by Accumulation of Plant Concretions.—Many algæ and aquatic mosses, as a result of their physiological activity, form rocky substrata. The latter are chiefly calcareous but some are siliceous. *Chara* plays the chief rôle in the formation of marl and is frequently found encrusted with it. Marl often accumulates in large amounts in ponds and lakes, where its action is to shallow the water. Calcareous concretions of travertine and tufa and siliceous ones of sinter or geyserite furnish initial areas for primary succession. They are formed by secretion from blue-green or green algæ usually about hot springs.

Reaction by Producing Weathering.—The primary reaction of plants upon rocks is the decomposition of the surface into an exceedingly fine soil. A secondary influence is the production and widening of cracks by means of roots and stems, but this is often lost sight of in the greater effects of atmospheric weathering. It is almost impossible, in many cases, to separate the effect of plants and atmosphere in the intimate decomposition of rock. All pioneers on rocks break down the surface in consequence of their excretion of carbon dioxide or acids and produce a fine layer of dust.[169] In the case of lichens and many mosses, this layer remains in place, but usually it is carried into cracks and crevices. This slow production of a thin soil or shallow pocket is reinforced by the decay of the pioneers themselves, which also materially increases the nutrient content and water-holding capacity. Here, again, it is almost impossible to separate the reaction of plants from weathering; but this is immaterial, since their effects are the same. The combined effect is to produce areas in which rock herbs can secure a foothold and to increase slowly the water content and nutrients.

The reaction through weathering takes place more readily when the rock is sedimentary and soft, especially if it is wet or moist during a large part of the growing-season. In such places, the pioneers are mostly mosses and liverworts, often preceded by algæ. Lichens are much less frequent and are apt to be collemaceous, *i.e.* of the gelatinous type. Water is abundant and the effect is chiefly to produce a foothold for herbs, apart from the increase of humus. As a consequence, the pioneer stages are often extremely short, and the rocky surface may be quickly covered with herbaceous or even shrubby vegetation.

When the rock is exposed to wind and sun, and especially when it is igneous, plant reactions begin with weathering by crustose lichens. The

substratum is changed to soil much more slowly and the sere is proportionately long.

Reaction upon Wind-borne Material.—This is the reaction that results in the formation of dunes and sandhills.[397] It is the outcome of the retardation of air currents by the stems and leaves of plants, especially pioneers in sand. The effect of the plant body is twofold; it is not only a direct obstacle to the passage of grains of sand but it also decreases the velocity of the wind and hastens the consequent dropping of its load. The same action likewise tends to prevent the wind from picking up the sand again and carrying it farther. The underground parts of sand plants exert a complementary reaction by binding the sand through the action of roots and rhizomes and by developing shoots which keep pace with the rise of the surface.[561] Certain pioneers form rosettes or mats, which hold the sand with such firmness that they cause the formation of hummocks with a height of 1 to many feet above the bare area.

The primary reaction on wind-blown sand is mechanical. The pioneer grasses, in particular, stop and fix the sand and produce stable centers for invasion.[239,577] This permits the entrance of other species capable of growing in bare sand, if it is not shifting actively. With the increase of individuals, however, the amount of organic material in the soil becomes greater, increasing the water-retention of the sand and the amount of nutrients. This is the primary reaction in sand areas after the sand binders have finished their work of stabilization. The reactions upon wind-blown deposits of loess must have been similar, although no deposits are known to be forming at the present time. Because of the smaller size of the particles, they were probably much more readily compacted by rainfall and also retained more water; hence, these loess areas were probably xeric for a much shorter time.

Reaction upon Water-borne Detritus.—The effect of plant bodies upon material carried by water is essentially similar to that noted for wind-blown sand. Stems and leaves slow the current and cause the deposition of its load in whole or in part. They also make difficult the removal of material once deposited, a task in which roots and rootstocks likewise have a share. This reaction is often associated with the deposit of sand and silt by the retardation of currents in rivers as they empty into bodies of water, but the effect of plants is usually predominant. Both processes cooperate to decrease the depth of water wherever plants occur in an area through which detritus is carried. The decreasing depth controls the usual sequence from submerged to amphibious plants. The latter continue the process but the movement of water is steadily impeded as the bottom rises, until finally it overflows the area only at times of flood. This sets a limit to the accumulation of detritus, and the further development is controlled by decreasing water content due to plant accumulations, transpiration, etc.

Reaction upon Slipping Sand and Gravel.—A characteristic feature of the Rocky Mountains is the steep talus slope known as a gravel-slide. The angle of the slope is usually so great that some slipping is going on constantly, while the movement downward is materially increased after a heavy rain. The fixation of such a slope is a problem similar to that which occurs in dunes and blow-outs. The coarse sand or gravel must be stopped and held in opposition to the downward pull due to gravity. The movement is slower and is somewhat more deep seated. Consequently, the species best adapted to gravel-slides are mats or rosettes with taproots or long branching roots. The latter anchor the plant firmly and the cluster of stems or horizontally appressed leaves prevents the slipping of the surface area. Each plant or each colony exerts the stabilizing effect for some distance below its own area, owing to the fact that it intercepts small slides that start above it. The primary reaction is a mechanical one, and a large number of species invade after the surface is stabilized. They increase the humus production and water content, and the subsequent reaction resembles that of all dry sand or gravel areas.

SOIL STRUCTURE

Plants modify the structure of the soil (1) primarily as a result of the admixture of plant remains following the death and decay of plant bodies and parts, *i.e.* the addition of humus. This reaction differs from that of accumulation of plant remains forming a new soil only in the lesser degree of accumulation and the greater decay. (2) They compact the soil and sometimes bring about the formation of a rocky layer within it. Finally, (3) they react upon soil structure by protecting it against weathering or erosion by water or wind.

Reaction by Adding Humus.—The change in texture of the soil due to the admixture of humus is caused by animals as well as by plants. In grassland and woodland soil, animals play the chief part in the distribution of the humus in soil. All plant communities produce humus in some degree by the death of entire plants, annually or from time to time, and by the annual fall of leaves and the aerial parts of perennial herbs, as well as by the decay of root hairs, root cortex, and frequently root branches of living plants. The amount produced depends upon the density and size of the population and upon the rate and completeness of decomposition. It is small in the pioneer stages of a sere, especially in xeric situations, and increases with each succeeding stage. It reaches a maximum in mesic grassland and in woodland.

The physical effect of humus is to make light soil more retentive of water and heavy soil more porous. Humus acts as a weak cement and holds together the particles of soil; thus, it serves both to bind a coarse-grained sandy soil and, by forming aggregates of the finest particles, to

render the texture of a clay soil more open. In general, it increases the water content of dry, bare areas and tends to decrease the water content of moist ones. The latter is chiefly the result of raising the soil level and is often complicated, as in bogs, by decreasing aeration and the possible production of harmful substances through partial decomposition. The effect of humus is most marked in the weathering of rock and in dry sand and gravel areas, where the action is cumulative throughout the whole course of development of vegetation. The increase in the number or size of the individuals in each successive stage results in more materials for humus production, and this increases the water content steadily from the initial to the climax stage. The ultimate effect in each stage is to favor the invasion of plants with greater water requirements and, hence, with greater powers of competition and duration. They readily become dominant and their predecessors disappear or become subordinate.

Reaction by Compacting the Soil.—This is an indirect effect due to the reaction of the community upon the water content. In the fine-textured soils of the Great Plains where rainfall is slight, the root systems of the grasses are relatively shallow but efficient in absorption. As a result, water penetration is usually limited to the surface 8 to 24 inches.[569] Much of the carbonates and colloidal clay have become concentrated at these depths, forming a densely compacted layer known as *hardpan*. Except for the presence of the vegetation, it seems probable that the hardpan would never have been formed.[464] Most deeply rooted species are also eliminated as a result of the hardpan except where penetration is increased by the activities of rodents, etc., and the short grasses tend to persist as the subclimax.

In many parts of Europe where heath grows upon sandy soils, there is formed a rock-like layer known as *ortstein* at a depth of 2.5 to 3 decimeters. The primary effect of ortstein is mechanical in that it completely stops the downward movement of solutes. It seems to have another influence apart from this inasmuch as roots grow poorly even when they pass through openings in the layer. The horizontal growth of roots is also found where the layer is not sufficiently compact to prevent penetration. This effect seems to be due to a lack of oxygen caused by poor aeration. Deeply rooted plants such as shrubs and trees can not grow on the area underlain with ortstein. Development is limited and the reaction results in the heath becoming a persistent subclimax.[196]

Reaction by Preventing Weathering or Erosion.—A plant cover, whether living or dead, everywhere produces an important reaction by protecting the surface from erosion. It has a somewhat similar effect upon the weathering of rocks by atmospheric agencies, but this has much less significance since the plants themselves are producing weathering. In the case of erosion, the reaction is much the same as when plants

stop drifting sand or suspended silt. In open communities, the stems and leaves reduce the velocity of the wind and water and make it difficult for them to pick up soil particles; in closed associations, the plants usually eliminate the effect of wind and water entirely and the erosion is null. The influence of cover is thus a progressive one from the sparse population of the pioneer stage, with most of the surface exposed to erosive action, through more and more closed communities to the climax. It is a stabilizing factor of first importance in that it prevents denudation and consequent initiation of a new area. At the same time, it assures continued occupation by the plants in possession and, hence, the continuance of the reactions which produce the normal sequence of stages. Its significance is clearly revealed when the cover is partially or wholly destroyed.

WATER CONTENT

Since water is the chief factor in succession, it is more or less affected by practically all reactions. In addition, the increase or decrease of water content may be the direct outcome of the activity of the plant itself.

Reaction by Increasing Water Content.—There seems to be no case in which flowering plants increase water content as a direct reaction. Their influence in reducing water loss from the soil is really due to the effect of shading. In the case of *Sphagnum*, however, the power of the plant to absorb and retain large amounts of rain and dew causes a direct reaction of primary importance. Because of this property, *Sphagnum* is able to water-log or flood an area and to deflect the sere or initiate a new one. In the moss areas themselves, the effect is essentially to produce a new area of excessive water content, which can be invaded only as the surface becomes drier. The ability of *Sphagnum* to retain water, either when living or in the form of peat, is also a controlling factor in the course of the development of the new sere.

The accumulation of plant remains as humus is the universal process by which the amount of water content is increased. No plant community fails to produce humus in some degree; hence, no soil escapes its action, though this is often small in the initial stage of xeric areas. Its influence is best seen in sand and gravel where the addition of a small amount of humus greatly increases its water-holding capacity. This is due to the minuteness of the particles of humus by which the aggregate surface for holding water is materially augmented and, partly, perhaps, to a direct power of imbibing water. The total effect is to decrease loss by percolation and evaporation and at the same time to increase the amount of non-available water. In more compact soils, humus at the surface decreases run-off by absorption and usually prevents excessive loss by evaporation in consequence of capillarity. Humus is also asso-

ciated with other reactions that affect water content, such as weathering, preventing erosion, and protecting against evaporation.

Reaction by Decreasing Water Content.—Plants decrease water content only by absorption and transpiration. An exception occurs in the case of certain fungi which form "fairy rings," notable on the Great Plains. The mycelium radiates outward in all directions by a slow forward growth and dies toward the center. This may continue for scores of years, the ring reaching many feet in diameter. The ring is marked by a circle of vegetation which is stimulated to a more luxuriant growth by extra nitrogen furnished by the decaying fungi. Just outside

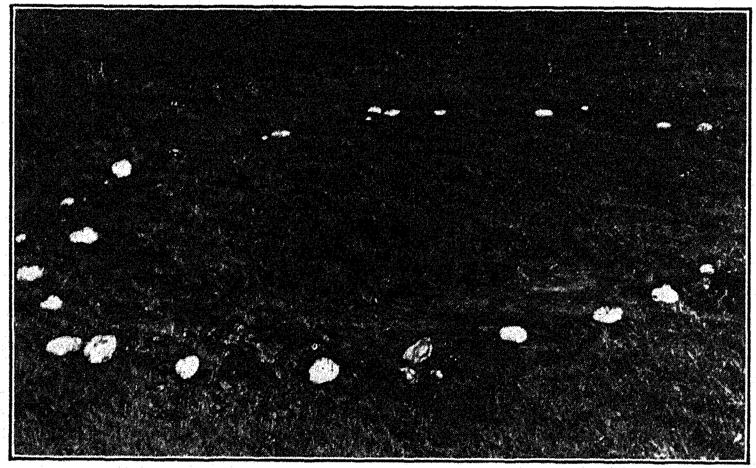

FIG. 94.—Fairy ring of a mushroom (*Agaricus campestris*) in a pasture. The bare area marks the place of greatest mycelial growth. The grasses have been closely grazed.

where the mycelium is active, it retards water penetration to such a marked degree that the area is bare[466] (Fig. 94).

Decrease of water by plant communities through transpiration is a universal reaction and is often critical in the case of seedlings of woody plants. This is characteristic of the ecotone between forest and grassland and plays an important part in the persistence of grassland subclimaxes as in the prairies and plains. Water content is also decreased as a result of other reactions. This is most striking in the shallowing of water by plant remains and by the deposition of silt in consequence of the obstruction of the current by vegetation.

NUTRIENTS AND SOLUTES

The reactions of plants that affect the soil solution are least understood. They are as follows: (1) by adding nutrients, (2) by decreasing nutrients, and (3) by producing acids and possibly toxins.

Reaction by Adding Nutrients.—This reaction is the direct consequence of the annual fall of leaves and the death and decomposition of plants and plant parts. In this way, a large supply of mineral salts is returned to the soil, and these are, sooner or later, freed to enter the soil solution. It seems clear that this process favors plants with a high nutrient requirement, but it may be negligible when there is an abundance of nutrients in the soil. The nitrogen relation is probably most affected. Available nitrogen depends almost entirely upon the activities of nitrogen-fixing and nitrifying bacteria and fungi and these, in turn, with the exception of symbiotic forms, upon the amount of humus. The whole question of nutrients really hinges on the amount returned each year and the amount already available in the soil. There is little evidence that humus plays an efficient rôle in succession apart from its fundamental relation to water content, but more experimental work is needed.[70] The partial or complete replacement of legumes by grasses and other herbs on areas where the raw subsoil has been laid bare is a nutrient (nitrogen) relation and is indirectly due to a soil organism (*Pseudomonas radicicola*).

Reaction by Decreasing Nutrients.—The inevitable effect of the absorption and use of solutes by growing plants is to decrease the total supply. Actually, however, this reduction is insignificant in nature and probably, also, in cultivation. The amount absorbed each year is a very small part of the total amount present—so much so that even cultivation may affect no appreciable reduction in 50 years.[211] Under natural conditions, all the nutrients absorbed are sooner or later returned. Nutrients, such as calcium salts, absorbed from the deeper soils, are, upon the death of the plant, deposited on the surface and in the reach of the seedling. Thus, the surface 3-inch layer of prairie soil is often richer in calcium than the layers immediately below. There is always slight loss of nutrients by erosion. In any event, there is no indication that successional movement is affected by the direct decrease of nutrients through absorption.

Reactions by Producing Acids and Toxins.—Wherever plant remains accumulate abundantly in water or moist places, access to oxygen is difficult. The decomposition is slow and partial, and the water or soil becomes more or less acid. In whatever way the various acids may be formed, lack of oxygen seems a necessary condition for their production. The effect of the acid upon plant growth is complicated with that of deficient aeration. Both, apparently, act together in diminishing the absorptive power of roots, probably in consequence of decreased respiration. This apparently is least harmful to plants with modifications for reducing transpiration, and acid areas are usually characterized by so-called "bog xerophytes" such as Labrador tea (*Ledum*), laurel (*Kalmia*), cranberries (*Vaccinium*), etc. It seems that most of the xeroid

species of wet places are not xerophytes at all but that a restricted group characteristic of peat bogs are actual xerophytes.

In so far as succession is concerned, the production of acids in swamps modifies the normal reaction of decreasing water content and marks a series of stages which dominate for a time, owing to a favorable response to poor aeration (p. 72). Whenever the latter is improved by draining, filling, or a drier climate, conditions become more favorable to species of neutral or alkaline soils, and the bog plants disappear in consequence of the change or as the outcome of competition.[310]

Soils of coniferous forests nearly always are acid and sometimes decidedly so. An admixture of hardwoods decreases acidity and in other ways greatly improves conditions in the soil.[162]

It is no longer thought that toxins are directly secreted from living roots, but there are a few cases where plants seem to exert a detrimental influence on the development of other species by the production of toxins during the process of decay.[182]

SOIL ORGANISMS

The relation of plants to the organisms in the soil is so complex that it is impossible to recognize all of the effects or to distinguish the causes of many of them. These organisms are either parasites living on the underground parts, symbionts, *e.g.* some forms of mycorrhiza in close relationship with these parts, or saprophytes living on the debris consequent upon the accumulation of plant remains. Animals as well as plants are included among soil organisms.

Reaction by Means of Parasites.—The relation between host plant and parasite is so intimate that it seems hardly to constitute a reaction, yet it has a direct bearing upon the fate of the community and its part in succession. If the parasitism is intense and destructive, as in *Pythium* and other "damping-off" fungi, the individual will be destroyed or handicapped in its competition for dominance. As a consequence, it may disappear wholly from the community, as in the case of the chestnut, due to blight, though this is relatively rare. The most usual effect is a decrease in number or dominance, and the species assumes a less important rôle. In the majority of cases, no direct influences are discoverable, the effect being merged in the general outcome of competition.

When the relation is more or less symbiotic, *e.g.* as in root-tubercule formation, its general effect is first to increase the dominance of the host plant but finally to favor species of higher nitrogen demands. Many legumes are able to grow in poorer soils and even in subsoil where the surface soil has been entirely removed, by virtue of their symbiotic partnership and consequent nitrogen production. They thus make possible the greater development of grasses before which they disappear,

so etimes completely.[70] The presence of mycorrhiza alone makes possible the successful ecesis of an increasing number of plants, especially trees and shrubs, and, hence, controls their appearance in succession.

Reactions by Means of Saprophytes.—These have to do chiefly with the formation of humus or with its modification in such a way as to make its components, especially nitrogen, again available for plants. This is true even of those fungi which exist in the soil as saprophytes and become parasitic when the proper host becomes available. A few of these are very destructive in their action and sometimes effect the complete disappearance of a dominant. The fleshy fungi, found everywhere in the ground layer of boreal coniferous to lowland deciduous forests, have to do largely with hastening the conversion of plant remains into humus, with its attendant effect upon water content, nutrients, etc. Puffballs and mushrooms of many species play a similar part in pastures and grasslands. This is also the well-known rôle of a large number of soil bacteria, especially those that liberate ammonia or elaborate nitrates from nitrogenous substances or fix free nitrogen. In the case of both fleshy fungi and bacteria, the final effect is to produce conditions in which plants with greater requirements can enter and displace those with less exacting demands. The same general effect is exerted by microscopic animals living in the soil. Some of the Protozoa play an antagonistic rôle by feeding upon bacteria.

AIR REACTIONS

The reactions of plant communities upon atmospheric factors are less numerous and usually less controlling than those upon the soil. An exception is the reaction upon light, which plays a decisive part in the later stages of the majority of seres. The effects upon the other air factors are so interwoven that it seems best to consider the reactions upon humidity, temperature, and wind together. As a consequence, the reactions may be grouped as follows: (1) upon light; (2) upon humidity, temperature, and wind; (3) upon local climate; and (4) upon aerial organisms.

Reaction upon Light.—The primary reaction upon light is seen in the interception of sunlight and the production of shade of varying degrees of intensity (Fig. 95). It has been held by some that the quality of light under a dense forest canopy is changed,[600] but it is now known that the light beneath the tree layer in most forests passes between the leaves and not through them.[287] Hence, the quality is unchanged. The reduction of light is slight or none in early stages of succession. Exceptions occur where plants are tall and dense, as in consocies of *Phagmites*, *Spartina*, etc., or where leaves or thalli are broad and spreading. As the population becomes denser, it intercepts more and more light, with the result that a subordinate layer appears. With the entrance of shrubs

and trees, the reaction steadily becomes more marked and the demarcation of subordinate trees more striking.

In a layered forest the reduction in light value is a progressive one from the primary layer downward. In many forests the cumulative reaction is so complete that the ground layer alone remains. As the canopy becomes denser, either by the growth of individuals or by the entrance of trees with closer tops, the layers begin to disappear. This usually takes place in a downward direction, the final stage of a closed formation containing only mosses, fungi, and saprophytic flowering plants, with occasional low herbs. Thus, even after establishment of a

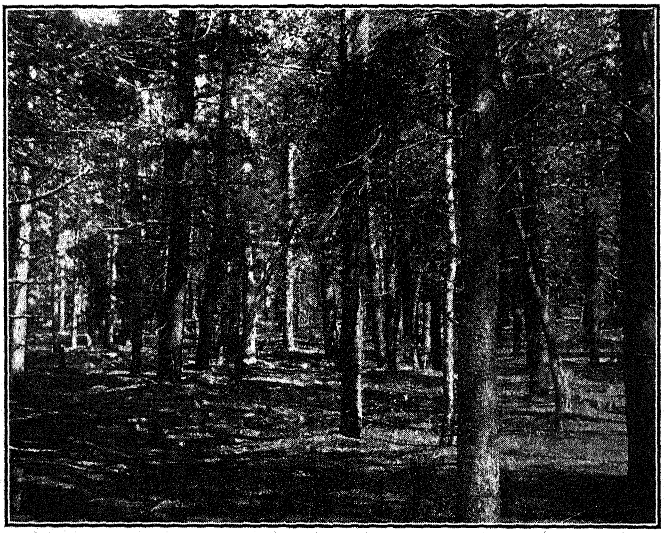

FIG. 95.—Reaction upon light. A rather open stand of lodgepole pine (*Pinus contorta murrayana*). Its inability to withstand shading is shown by the dead branches.

dominant species of a climax stage, there may still be a successional disappearance of subordinate layers.

The most important effect of the reaction upon light is shown in the succession of dominants after one or more have secured the controlling position with respect to light. This is most clearly shown and is best understood in the case of trees, but it is true of shrubs and in some degree of grasses and herbs. To maintain itself, a forest tree is confronted by the twofold task of being able to grow in both sun and shade. If it is the first tree to invade, the crucial test comes when it has reacted upon the light in such a way as to make it necessary for its seedlings to ecize in the shade. This is the test in which practically all pioneer forest trees fail. The species which invade the pioneer forest must grow in reduced light intensity for a long time, until the individuals stretch above the original trees. The change of the leafy top from shade to sun is an

advantage, however, and it marks the beginning of the disappearance of the trees of the first forest stage. The reaction of closer growth, denser crowns, or both, decreases the light still further, with the result that the seedlings now meet a severer test than did those of the preceding generation of the same species. In most cases, they are able to establish themselves, but in smaller number and with reduced vigor. They are placed at a disadvantage in competing with seedlings that endure deep shade. When these enter, they soon gain the upper hand, reach up into the dominant layer, and gradually replace the species already in occupation. In most, if not all, regions with a climax forest, this process may be repeated several times, one associes succeeding another, until the species whose seedlings endure the lowest light intensity are in final possession.

Reactions upon Humidity, Temperature, and Wind.—These three factors are necessarily linked together because of their direct effect upon the plant through transpiration and the indirect effect through evaporation of soil moisture. The plant community reacts directly upon each factor, *e.g.* woodland decreases wind and lowers summer temperature and also increases humidity, but the response of the plant is controlled by humidity. The reaction of a sparse pioneer population is more or less negligible, but the increasing density and height of individuals brings about a measurable result which becomes significant in most closed associations, especially those of shrubs and trees.

In layered forests, the reaction is greater in or beneath the ground layer, where it consists of herbs. Humidity is directly increased by transpiration, but the effect is cumulative because the moisture-laden air is not carried away. The heat rays are absorbed or reflected and the lower temperature that results causes an increase in relative humidity. The capacity of the air for moisture is correspondingly decreased and both transpiration from the plants and evaporation from the soil surface are reduced. The final effect is to make the water content more efficient and thus essentially to increase it. The general effect of the reaction is the same as that of increasing humus, and the two are indistinguishable, as a rule. The reduced evaporation from the soil surface, and, perhaps, from the seedlings as well, is a critical factor in the ecesis of many seedlings, especially those of trees.

Reaction upon Local Climate.—Plant communities react upon the air above them by transpiration and by lowering the temperature. As a consequence, they receive more soil moisture as dew and rain than do bare areas. This reaction of vegetation is measurable only in the case of forest and scrub but probably occurs in some degree in all vegetation, particularly in the formation of dew. Forests increase both the abundance and the frequency of local precipitation over the areas they occupy, the excess of precipitation as compared with that over adjoining unforested areas varying from 1 to more than 25 per cent. At Nancy, France,

the average increase in forested areas for 33 years was 23 per cent, and in Germany and India it was computed to be 12 per cent. The percentages of rainfall in the center, on the edge, and outside the forest were 100, 94, and 77, respectively.[605] Some meteorologists are inclined to ascribe a part of the differences in the amount of precipitation over forest and open fields to failure of the rain gages to record the actual precipitation, especially in a wind. The evidence with improved rain gages, however, shows clearly that forests greatly increase the amount of precipitation.

The influence of forests upon local precipitation is more marked upon mountains than in the plains and it rapidly increases with altitude. At elevations less than 300 feet the effect was only about 1 per cent, while at altitudes of 2,000 to 3,000 feet it ranged from 19 to 84 per cent. Denuded mountains often fail to cause moisture-laden winds to precipitate their moisture. A most direct proof of the effects of forests in increasing local precipitation is afforded by observations following forest planting as in the prairies or steppes of southern Russia. More than 5,000 acres of forests were planted at various times. When the trees were 30 to 48 years old, precipitation was determined within and without the forested area. In the forest it was 16 to 24 per cent greater. These results are in accord with numerous other investigations in various parts of the world. There is some evidence that rainfall is appreciably greater over coniferous than broad-leaved forests.[605]

Forests transpire enormous amounts of water. An acre of mature oak trees absorbs 2,000 to 2,600 gallons per day.[605] The large amounts of water transpired by forests contribute greatly toward increasing the moisture content of the atmosphere above. Hence, the air over forests contains a much larger amount of moisture and is consequently cooler than that over a bare area or one covered with herbaceous vegetation. If all the moisture given off by the forest could be made visible as a fog, heavily forested areas would appear enveloped by a damp mist, more dense over coniferous than over broad-leaf forests. The condensation of vapor on the surface of leaves as dew or hoarfrost is much less than an inch per year in northern latitudes but increases in southern latitudes and especially in tropical forests. In damp, tropical forests, so much moisture is condensed that during clear, still nights drops of dew fall continuously from the leaves as in rain. A similar phenomenon occurs in the redwood belt on the Pacific Coast.

Reaction upon Aerial Organisms.—The lichen population of the trees in an open yellow-pine forest is typically very different from that of a dense forest of Douglas fir or white fir. The difference in the occurrence of these and other epiphytes such as orchids, etc., as well as parasitic organisms, *e.g.* mistletoe, may be due either to the presence of a particular host plant or matrix or to the reactions of the trees in reducing light and wind and increasing humidity. Usually, the two effects are correlated,

the presence or success of the parasitic or epiphytic organism being affected by the conditions as well as controlled by the host plant or matrix. This reaction is characteristic of communities with a dominant canopy, such as a forest or thicket, but obtains in some degree in all vegetation. It not only affects plants directly but also the presence and behavior of pollinating insects.

A Study of Reactions.—Make a study of an area where forest or scrub has replaced grassland or where the reverse change has occurred, as a result of cutting or fire. Make a detailed list of the various kinds of reactions that have occurred as a result of the change in plant populations.

STABILIZATION AND CLIMATE

The progressive invasion typical of succession everywhere produces stabilization. The habitat has been occupied for longer or shorter periods by the populations of the several stages in the sere. From the beginning, there has been a continuous stream of invaders and the development of the formation, like the growth of any organism, has been continuous. Where the dominating newcomers were of a different life-form from the previous occupants, the change stood out clearly, as when floating plant consocies were replaced by those of reed swamp. The particular stage persisted just as long as the new life-form was able to produce a reaction sufficient to control the community. Due to reactions, the habitat is constantly brought nearer medium or mesic conditions. The vast majority of species are not pioneers, *i.e.* xerophytes or hydrophytes, but mesophytes with comparatively high but balanced requirements for ecesis. The final outcome in every sere is the culmination in a population most completely fitted for the mesic conditions brought about by the reactions of past plant generations. Such a climax is permanent because of its entire harmony with the stable habitat. It will persist just as long as the climate remains unchanged, always provided that migration does not bring in a new dominant from another region.

In many cases, dominance is primarily due to the control of water content as in grassland, or of light as in reed swamp, or of both as in scrub. Thus, the essential cause of the temporary stabilization with each change of life-form is dominance. But until the final stage of development is reached, the populations are held in a certain stage only until the reactions become distinctly unfavorable to them or until the invasion in force of a superior life-form. Thus, reaction is not only the cause of dominance but also of the loss of it. It makes clear why one community develops and dominates for a time, only to be replaced by another, and why a stage able to maintain itself as a climax finally appears.

Stabilization is increase of dominance. Every complete sere ends in a climax, *i.e.* a point is reached when the occupation and reaction of a dominant is such as to exclude the invasion of another dominant. The

climax is thus a product of reaction operating within the limits of the climatic factors of the region concerned. The climate determines the dominants that can be present in the region and what life-form will constitute the final stage of development of the formation. Thus, climate is a stabilizing cause of succession. Reaction determines the relative sequence of stages and causes the selection of one or more of the final dominants. The climax is the mature or adult stage of vegetation. The climax formation is the fully developed community, of which all initial and medial communities are but stages of development. The causes

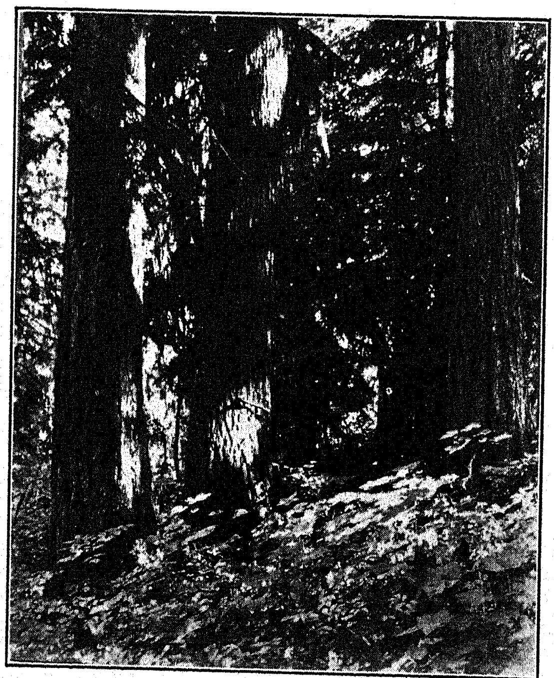

FIG. 96.—Forest of tamarack (*Larix*), white fir (*Abies*), and white cedar (*Thuja*), Idaho.

that retard the complete maturing of the organism by handicapping or destroying some stage have been pointed out in discussing the subclimax.

Although the climax marks the close of the general development, its recognition is possible only by a careful study of the whole process. Duration is in no wise a guide, since even pioneer stages may persist for long periods, and medial stages often appear to be climax. Development should be traced in all parts of the climatic region where dominants occur which are similar to the one supposed to be climax. Once attained, the climax will persist, except for catastrophies such as fire, flood, landslides, etc., until there is a fundamental change in climate, or until an essentially new flora develops as the outcome of long-continued evolution (Fig. 96).

CHAPTER IX

FACTORS OF THE HABITAT; THE SOIL

The habitat, *i.e.* the kind of place in which plants grow, is marked by development similar to that of the formation. When, moreover, the plants within a community are examined as individuals, it soon becomes apparent that life conditions within the common habitat of the community are much diversified. Plants growing side by side (*e.g.* bluegrass and goldenrod or bur reed and water plantain) are not subject to exactly the same conditions. The immediate environment of the two may differ more or less as to water content, nutrients, light, temperature, humidity, wind, and other factors. Furthermore, if the environment of a single species is critically examined, it will usually be found to be far from uniform. During the early stages of development, seedlings, especially of trees and other tall-growing plants, and rosette forms, as those of evening primrose, occupy a very different habitat from that of the mature plants of these species. This is true both above and below ground, for soils are usually very different with increasing depth as regards water content, nutrients, aeration, etc., and the developing root, like the shoot, lives in several partial habitats.[598] Thus, the term habitat has come to have both a general and a more limited and specific meaning.

Factors of the Habitat.—Every part of the environment that exerts directly or otherwise a specific influence upon the life of the plant is a factor of the habitat. The habitat factors are often grouped into four general classes: climatic, such as temperature, precipitation, etc.; physiographic, such as slope, surface, and other topographic factors; edaphic, *i.e.* those pertaining to soil; and biotic, the effect of man and other organisms. Such a classification, however, is quite artificial from the standpoint of the plant and vegetation and consequently will not be used.

The habitat is a complex in which a factor acts upon other factors and is, in turn, acted upon by them. Plants show the effects of an increase or a decrease in factors by functional responses (*e.g.* decreased photosynthetic activity in shade), by differences in growth, and by changes in structure (Figs. 97 and 98). Species vary widely in the nature and degree of response. But only certain factors are the direct causes of plant response, while others can affect the plant only through the former. Water, humidity, light, solutes, and soil air are direct factors of first importance because of their variation from habitat to habitat. Other direct factors, such as carbon dioxide, oxygen, and gravity, are negligible because of

their constancy. Temperature is both direct, as in its effect upon metabolism, and indirect. But its indirect action through the water relation, *i.e.* accelerating or retarding absorption and transpiration, is usually the most tangible. Other factors are indirect or remote.

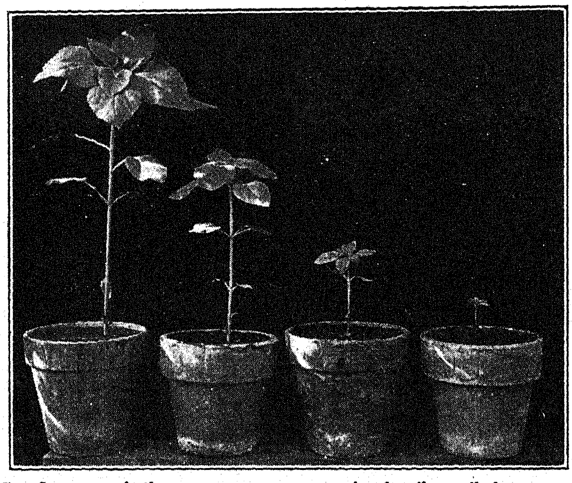

FIG. 97.—Sunflowers of the same age grown in fertile soil but receiving different amounts of water. That on the right was given just enough from a graduate each day to keep it alive, the next received twice this amount, the third four times, and the largest eight times as much.

Habitat factors fall naturally into three groups: (1) those that affect the activities of the plants directly; (2) those that exert an indirect effect; (3) and those whose effect is only remote and is exerted usually through an indirect factor. This grouping does not include biotic factors which are of such diverse nature that they will be considered separately.

DIRECT FACTORS	INDIRECT FACTORS	REMOTE FACTORS
Water content	Temperature	Altitude
Humidity	Precipitation	Slope
Light	Soil composition	Exposure
Solutes	Wind	Surface
Soil air	Pressure	

Absorption is primarily dependent upon water content, transpiration upon humidity and temperature, and photosynthesis upon light. Solutes directly affect plant nutrition, and soil air is essential for respiration of most roots. Precipitation and soil composition indirectly affect absorption by modifying water content. Temperature, pressure, and wind indirectly affect transpiration through their influence upon humidity. The physiographic factors are all remotely related to vegetation. Slope and surface modify water content through their effect upon precipitation. Altitude, acting through temperature and pressure, modifies humidity.

Light is reduced in cloudy regions, a condition frequently resulting from the effect of altitude and slope on temperature and wind. Numerous other interrelations occur. Although the environmental factors are closely interwoven, those directly affecting the plant are few.

Since the underground parts of plants are quite different from the aerial ones, because of the very different environment in which they grow, the soil and air habitats will be considered separately. In a following chapter, it will be shown how these parts are adapted to and modified by the soil environment.

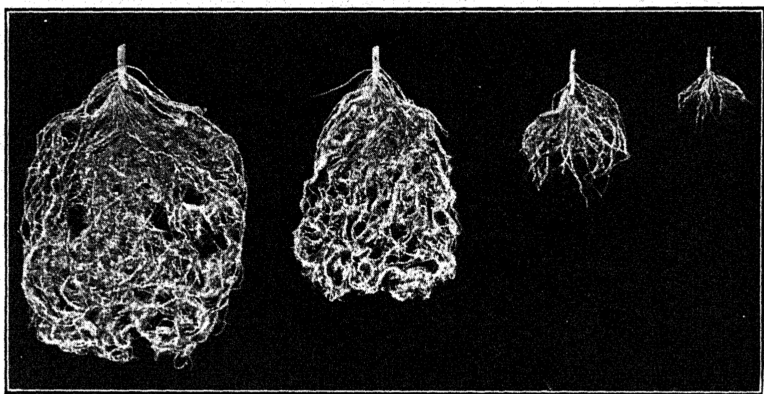

FIG. 98.—Root systems of sunflowers shown in Fig. 97.

Edaphic Factors.—Edaphic factors are those pertaining to the soil. Some, like water content and solutes are direct factors, soil composition is an indirect factor, and the slope of the land is a remote one. Nearly all higher plants except parasites and epiphytes are rooted in the soil (Fig. 99). The latter do not depend on the soil directly but secure nutrients or support from plants thus anchored.[304] Even floating water plants secure the necessary soluble salts that have been dissolved from the soil. This partial environment, the soil, often contains and reacts upon a much more extensive portion of the plant body than does the atmosphere. The principal edaphic factors are water content, soil air, solutes, and temperature. These are all so closely related to the physical constitution and properties of the soil, *viz.* texture, structure, and humus content, on the one hand, and its chemical nature, on the other, that to understand the relationship brief consideration need be given to each.

Nature and Origin of Soil.—The soil is the unconsolidated upper few feet of the earth's crust, which through processes of weathering and the incorporation of organic matter has become adapted to the growth of plants. In a general way, the term soil is applied to the layers inhabited by the root systems of plants, which may extend to depths of only a few inches to more than 20 feet.

The chief component of most soils is derived from rocks. More than 90 per cent by weight of ordinary air-dried soil consists of rock fragments.

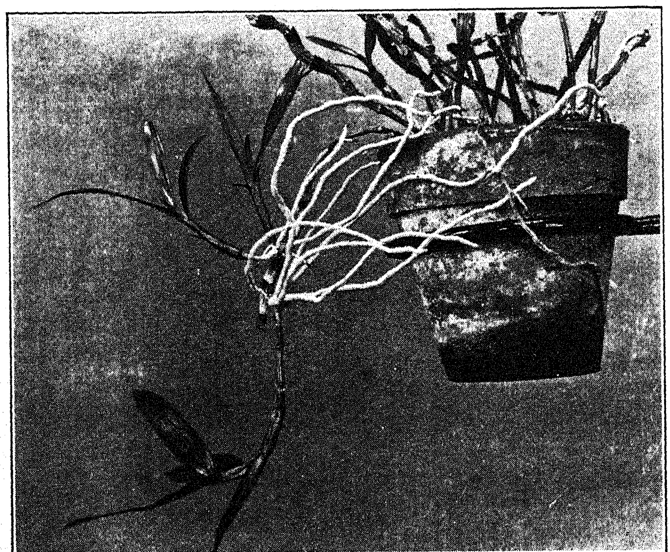

FIG. 99.—An orchid (*Dendrobium*), showing aerial roots covered with white velamen. This is a modification of the epidermis consisting of layers of dead cells which readily absorb water during rains, etc. (*After Gager, General Botany, P. Blakiston's Son & Co.*)

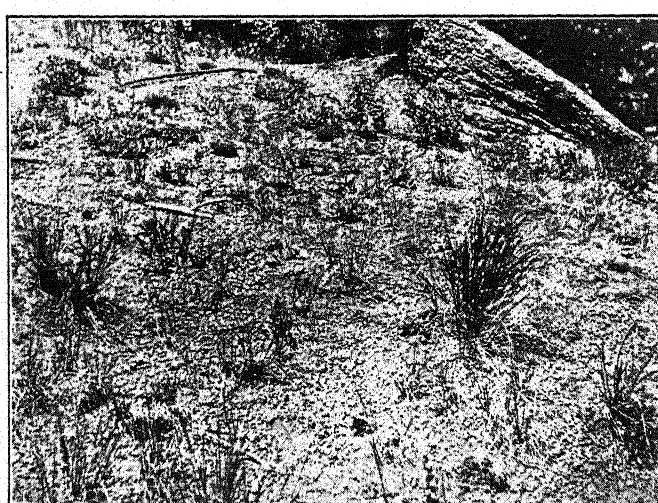

FIG. 100.—Decomposition of a granite boulder into gravel and sand and the further breaking down of these by the roots of herbaceous plants.

The small, angular fragments have been derived from the rock and possibly later transported by wind or water (Fig. 100). During the past centuries, rocks have disintegrated and are now disintegrating by

the action of such forces as alternate freezing and thawing, formation of ice in pores and crevices, erosion by wind and running water, surface scouring by glaciers, and the prying and dissolving action of roots and rhizoids. Accompanying this process of fragmentation has been the exceedingly important process of chemical corrosion or decomposition, for plants can not grow in rock fragments, no matter how small the particles, unless the nutrients locked in these particles as insoluble compounds have been changed chemically to water-soluble substances. The latter alone can be absorbed by the roots. Throughout the whole process of soil formation, plant and animal residues have been converted, largely by the activities of microorganisms, into the dark-colored organic matter of the soil. The total organic matter or humus of a mineral soil constitutes from less than 1 to more than 15 per cent of its dry weight.

The same physical forces that have weathered the rocks have, in most cases, moved the fragments to other places to form soils. Hence, the soil instead of being residual, *i.e.* formed in place, is usually transported. According to the agencies that carry the materials, soils are classified as gravity laid or colluvial, *e.g.* at the foot of steep slopes and in mountain valleys; wind laid or æolian, *e.g.* loess, dune sand, adobe; glacier laid; and water laid. The last are alluvial if along streams, lacustrine in old, deep lake beds, and marine if along sea coasts. Other soils are formed largely by the accumulations of organisms. These are called peat if mostly organic and so poorly decayed that the plant structures may still be identified and muck if the plant tissue has lost its identity or the soil contains more mineral matter.

Formerly, great stress was laid upon the kind of rock from which the soil originated. Rocks may be grouped as igneous or heat formed (*e.g.* granite, basalt); sedimentary or water laid (*e.g.* sandstone, limestone, shale); or metamorphic, that is, modified by heat, pressure, and chemical change (*e.g.* gneiss from granite, marble from limestone, quartzite from sandstone).

The chemical and physical characters of soils are determined, at least for a time, by the kinds of rocks from which they are derived. Soil derived from sandstone, for example, has much coarser particles and, consequently, a lower water-holding capacity and better aeration than the clay derived from limestone. The latter, moreover, is rich in calcium carbonate, but the former has little or none. Clearly, these factors have a profound effect upon the vegetation growing on the two types of soil.

Soil Texture.—Soils differ a great deal in the relative fineness or coarseness of the particles of which they are composed. Texture is that property which has to do with the relative proportions of particles of different sizes. Of the three general groups of soil particles the coarse ones are sand, those of medium size are silt, and the very fine particles

are clay. The actual diameters of the various particles are shown in Table 4. The relative amounts of these different grades of particles in a soil determine its texture. It is the effect on the total surface of soil particles that makes texture important as a soil property. The finer the particles the more surface is presented for the retention and solvent action of water and the greater is the absorbing area for plants. For example, coarse sand grains are 0.5 to 1 millimeter in diameter, but clay particles are so small that it requires approximately 65,000,000 of the largest of them to equal one grain of sand.[353] The clay particles are so finely divided that they exhibit the properties of matter in the colloidal state, one of which is an exceedingly great water-retaining capacity. The surface area presented by a single cubic inch of clay is 10 or more square feet, that of coarse sand only about 100 square inches.

With respect to texture, soils may be grouped into a number of classes such as sandy, sandy loam, clay loam, or clay. The class to which a soil belongs can be closely approximated by examination in the field and determined accurately by mechanical analysis. This consists of separating the soil into the grades of particles of which it is composed and determining the percentage of each. The coarser sands are separated by means of screens, the fine sand, silt, and clay, in water under the action of gravity. The texture of two very different soils is shown in Table 4.

TABLE 4.—DIAMETER AND PERCENTAGE OF VARIOUS SOIL PARTICLES AND THE TEXTURE OF A SILT-LOAM AND A FINE SANDY-LOAM SOIL

Source of soil	Fine gravel, 2 to 1 millimeter	Coarse sand, 1 to 0.5 millimeter	Medium sand, 0.5 to 0.25 millimeter	Fine sand, 0.25 to 0.10 millimeter	Very fine sand, 0.10 to 0.05 millimeter	Silt, 0.05 to 0.005 millimeter	Clay, less than 0.005 millimeter
Upland prairie, Lincoln, Nebr................	0.0	0.3	0.5	1.6	19.8	48.6	29.2
Forest nursery in sandhills, Halsey, Nebr.....	0.4	4.3	9.3	57.1	19.5	7.6	1.8

The chief component of the first sample is silt, and because of its desirable proportions of sand and clay and good humus content, it is designated as a silt loam. It has a high capacity for holding water—about 60 per cent of its dry weight. The second is a fine sandy loam with a relatively low power of water retention, only about 30 per cent.

Soil texture not only exerts an important effect upon the water relations but also upon aeration as well as the supply of nutrients. It profoundly affects the rapidity of the processes of decay of organic matter and its retention against leaching. The nitrogen content of a soil is closely related to its texture.[418]

Soil Structure.—Structure is a term expressing the arrangement of the individual grains and aggregates that make up the soil mass. The irregularity in size and shape of the rock particles prevents tight packing and affords open, irregular spaces through which air and water can circulate, while their weight and mutual pressure furnish the necessary resistance for firm root anchorage. Soils of single-grain structure like sand, where the particles function more or less separately, are fairly simple. But a very complex structure is represented in clay where the soil granules or crumbs are composed of many particles bound together by colloidal or glue-like material originating from the finest clay and humus

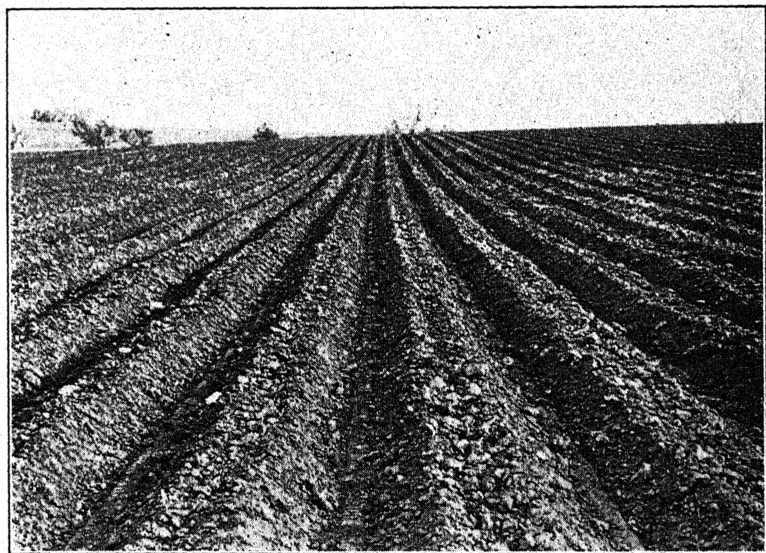

FIG. 101.—A field that has been listed and planted with corn. It has a fairly good soil structure. The corn grows slowly in the mineral soil at the bottom of the lister-rows and receives more water than if surface planted. By repeated cultivation, the furrows are filled and the soil finally ridged up against the rows of corn.

particles. A rich loam usually furnishes an example of a soil with an excellent structure. Some of the particles are large and function as individuals. Those of smaller size form a nucleus about which the still smaller particles aggregate into granules, a process termed *flocculation.* This aggregation of the smallest soil particles into groups or crumbs which act as individuals makes the soil much more porous. The larger interspaces permit the water to drain away as they become filled with air, while the smaller ones retain moisture. Humus has a very important effect in lightening the soil and promoting a good soil structure (Fig. 101).

The structure of a soil determines its porosity. This, in turn, affects the absorption of water and, therefore, run-off and often the consequent erosion. The movement and storage of water in the soil and soil aeration

are also affected. Water content and aeration, as well as compactness of soil, all profoundly affect root development. A good soil structure is maintained in nature by alternate wetting and drying, by freezing and thawing, by the action of organic matter and lime, and by the mechanical action of plants and burrowing animals. Poor structure is produced by the puddling action of rain on bare soil surfaces, poor drainage, alkali, etc.

The importance of roots in maintaining a good structure is often overlooked. As a result of the interlacing and clutching of earth particles by myriads of roots, the soil is compressed into granules whose identity, stability, and permanence are established by a surrounding colloidal film of humified root material.[416] Where the virgin prairie sod is first broken, it is mellow, moist, and rich. But after a few years of cultivation there occurs a great change in its physical condition. It becomes more compact, dries more quickly, bakes more readily, and often forms lumps and clods. But when grass is again grown for a few years, perfect tilth and freedom from clods are regained. The soil particles are wedged apart in places and crowded together in others. The small soil grains become aggregated together into larger ones. Each year many of the old roots die and are constantly replaced by new ones. The soil is filled with pores and old root channels; the humus from decaying vegetation helps cement soil particles into aggregates and thus lightens and enriches it.[525]

The action of burrowing animals on soil structure is also important. Earthworms play a significant part. Their activities, in semiarid regions at least, are not confined to the surface layers. They sometimes penetrate to a depth of 10 feet. There are frequently thousands of them per acre. Burrowing everywhere, dragging down large vegetable fragments from above, they help to aerate the soil and keep it light. Rodents, ants, and various other animals mix and open up soil and subsoil and thus promote root penetration. On the "hard lands" of the Great Plains, rodents have had an important effect upon soil structure, increasing water penetration and thus permitting the growth of certain deeply rooted species of plants. Insects, insect larvæ, nematodes, and hosts of other organisms abound; all are instrumental in loosening the soil and thus affecting root development and plant growth.

Humus and Microorganisms.—Humus comprises the more or less decayed organic portion of the soil. It is mostly but not entirely vegetable matter, dark in color, light in weight, and more or less intimately mixed with the other soil components. Locally, decaying animal remains or feces may make up an appreciable amount and may even form the bulk of the soil, as in places inhabited by dense colonies of birds or small mammals. All soils that support vegetation contain humus. The amount may be very small in newly formed soils such as wind-blown sand that supports only a sparse plant population, but it increases with the development of the sere.

To Determine the Amount of Organic Matter in a Soil by Loss on Ignition.—Select samples of soils from several habitats representing different stages of a sere, such as grassland, scrub, forest, etc. Samples should be taken to the same depth in duplicate and each sample very thoroughly mixed. Place about 5 grams of the dry soil in a crucible of known weight when oven dry. Heat in an oven at 110°C. for 3 hours or more, cool in a desiccator, and weigh very accurately. Ignite in a furnace or over a large burner at a low red heat until the organic matter is all oxidized. Cool again in a desiccator and reweigh. Calculate the percentage of humus based on the dry weight of the soil. This simple method, although widely used, is open to objection, since it sometimes gives results that are too high.

Based on dry weight, the organic matter of a mineral soil may constitute from less than 1 to more than 15 per cent of the soil. These low percentages are due to the fact that the mineral-soil matrix has a density about three times as great as that of the humus. Relative to volume, the humus may constitute 4 to 12 per cent and the mineral-soil components only 41 to 62 per cent, the remaining volume being pore space which is occupied by water and air.[419] The amount of humus varies with the climate. Arid soils contain less, partly because there is less vegetation from which it may form, and partly because of its too rapid oxidation. For example, fine-textured soils in Washington under 20 inches of rainfall have more than four times as much humus as soils of similar texture under 8 inches of precipitation.[493] Similarly, soils of the short-grass plains of western Nebraska under 16 inches of rainfall have only about 58 per cent as much organic matter as tall-grass prairie soils of the same texture under 30 inches of precipitation in the eastern part of the state.[418] Conversely, in soils that are very wet, decay is greatly retarded and plant remains may accumulate in such quantities as to constitute 85 per cent or more of the weight of the soil. This is the case in peat or muck.

Although much of the humus has its origin from aboveground plant parts, large amounts are formed from root decay and a smaller amount from the remains of soil organisms. In the production of organic matter in soils, two processes are involved, the furnishing of organic materials by plants and its decay by soil organisms. Plants, of course, return more to the soil than they have taken from it, since a large part of their body is made from the products of photosynthesis. The decay of the organic debris is brought about almost entirely by the activities of various groups of bacteria, fungi, Protozoa, and other inhabitants of the soil.

The first organic materials to disappear are the sugars, starches, pentosans, pectins, celluloses, and proteins. Their decomposition results in the synthesis of a proportional amount of microbial protoplasm.[548a,549] In fact, the nitrogen and mineral residues such as phosphates, potassium, and calcium, made available by the decomposition of plant remains, may again be largely utilized by the microorganisms and released gradually upon their death and decay. Only a small part may at once be made available to the growing plant. This is fortunate, since otherwise the

rapidity with which organic matter is decomposed would result in the liberation of nutrients which would be either largely lost to the atmosphere or leached beyond the root horizon. Other organic materials such as lignins, fats, waxes, etc., are decomposed much more slowly by soil organisms.[549]

In the presence of air, oxygen is slowly but continuously absorbed during the process of decay and an almost equal volume of carbon dioxide evolved. The organic materials are finally broken down into simpler compounds, the end products being carbon dioxide, water, ammonia, methane, and inorganic compounds of sulphur and phosphorus. The ammonia is immediately oxidized to nitrous and then to nitric compounds, which occur in the soil as nitrates. The process of decay, however, is not one of immediate simplification. The various organic acids, etc., originating as intermediary products, react upon the minerals with which they are in contact, and these may thereby be made soluble and available to the plant. During humus formation, the materials take on the characteristic dark color.

Thus, the humus that is constantly formed is continually being broken down. Various stages in its decomposition are always in progress. It becomes an important source of nutrients for plants and there is thus a close relation between the vegetation and the soil organisms. The latter are dependent almost entirely upon growing plants to furnish materials upon which they live, while vegetation is equally dependent on the activities of the soil organisms for removing the residues of previous generations of plants and for the continued production in the soil of simple materials which are necessary to its growth.[419] The enormous importance of this process in the economy of nature is evident and the importance of the rôle of soil organisms can scarcely be overemphasized. Except for the work of the wrecking crews composed of myriads of microscopic organisms, which immediately attack the fallen vegetation and reduce it to water-soluble and, hence, usable compounds, plant residues would be distinctly detrimental to the soil.

The decay of organic matter takes place most rapidly in warm, moist, well-aerated soil, *i.e.* under conditions most favorable to the development of the organisms carrying on these processes. Raw humus is an accumulation of litter in cold or dry soils or those with an acid or alkaline reaction unfavorable to the growth of organisms causing decay. Certain forests and heaths of cool climates have soils of this type where the disintegration of the humus proceeds very slowly. Where organisms causing decay are excluded because of poor aeration, the plant bodies accumulate as peat. The structures of the dead plants or parts of plants forming the peat are often preserved (Fig. 93).

The effect of humus in improving the physical condition of the soil is marked. It acts as a weak cement to bind sand, lightens or opens

a clay soil by separating the particles, and thus increases percolation, aeration, bacterial activity, and ease of root penetration. Being very absorbent, it helps to retain water so that in regions of moderate rainfall vegetation growing in soils rich in humus is less likely to suffer from drought. In fact, its physical effects are so marked that when the organic matter present in a soil is very high the distinctions between sands, loams, and clays are practically obliterated. Soils that have lost humus are harder than formerly and in poorer tilth; they crack easily and expose great surfaces to evaporation.

The Soil Solution.—An analysis of water that has drained through a soil shows that it contains a great many substances which have been dissolved. Certain portions of the soil have gone into solution. The soil solution is very dilute, its concentration ranging from 0.05 to 0.2 per cent in ordinary cultivated soils. It is from this solution that plants obtain their mineral nutrients. The soil solutes originate from several sources. Some are formed by the dissolving of portions of the original rock particles; some come from decaying humus; others are built up by bacteria and other soil organisms; and still others are excreted by roots. Oxygen and carbon dioxide are important dissolved gases.

The soil solution is variable in its composition, partly because of the variability of the solvent power of the water, which, in turn, may depend upon its carbon-dioxide content, and partly because of the nature and amount of soil colloids. The soil colloids of finely divided humus particles and clay form a gelatinous coating over the surface of the rock particles. They retain the solutes by adsorption. The amount thus retained varies with the amount of water, partly adsorbed and in surrounding films. The more water present the more solutes go into solution. As the water increases, however, the concentration of the solution decreases. Root hairs with their gelatinous walls are in immediate contact with the soil particles. Due to precipitation, absorption by the roots of plants, evaporation, and drainage, the water content is always changing. Vegetation, moreover, is constantly removing nutrients, and other amounts are lost by leaching. The activities of microorganisms continuously alter the amount of nitrates and this, in turn, affects the amount of dissolved bases. The soil solution is constantly changing in both composition and concentration. It contains the reserve nutrients, and as these are absorbed by plants, new supplies are liberated from the colloidal soil complexes.[239a]

Although over 30 elements have been found in the ash of plants, experiments with plant cultures have shown that only a few of these are essential to normal growth. This was determined long ago by adding various soluble salts to pure distilled water or water in clean quartz sand and observing the effect upon growth and yield. Such studies show that for normal growth plants need only the soluble salts of

nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, iron, and sometimes chlorine. Recently, it has been found that minute traces of other elements such as manganese and boron[50] are also essential, the necessary amounts apparently having occurred as impurities in the chemicals used in the earlier experiments.[344,503,504]

Nearly all natural soils contain these elements in sufficient amounts to promote a good growth of vegetation. Only certain "sterile" sands, which consist almost wholly of silica, and a few other types of soil are really deficient in the necessary nutritive elements. Most unproductive sands are, moreover, unfavorable to vegetation, not because they are deficient in nutrients, but because they can not retain a sufficient supply of water. Where land is continuously cropped, the addition of nutrients and especially nitrates as fertilizers greatly increases yields. The amount, however, must be in accord with the water supply. If the plants are stimulated to a luxuriant growth when water is abundant, they are greatly harmed by subsequent drought.

In native grasslands, nitrates are used as rapidly as they are formed. With rare exceptions, there is never an excess. When the soil is warm and moist and the plants are growing rapidly, nitrates are elaborated rapidly but not excessively, and the plants thrive. As the soil becomes dry and the plants begin to suffer, nitrification diminishes, and thus the plants are automatically saved from excessive nutrients in time of drought.[416] Different species of plants remove the various nutrients in different amounts. These differences are due both to the extent and to the degree of branching of the roots and to variations in their absorptive activity. Under natural conditions, the materials removed from the soil by growing vegetation are ultimately returned in plant remains or animal excretions. Those washed down into the deeper soil are often brought to the surface again through absorption by deeply penetrating roots. Certain soil constituents such as nitrogen compounds and calcium carbonate are easily leached out and large amounts lost annually in drainage water, but those of potassium and phosphorus are almost entirely retained in place by adsorption by the soil colloids. Thus, soils of arid and semiarid regions, occupied largely by grassland or desert vegetation, are potentially richer than well-leached soils in more humid regions.

DEVELOPMENT OF SOILS

Soils undergo a process of development, the controlling factors being climate and vegetation. The features assumed by the soil in its development from infancy through youth, maturity, and old age vary with the environment. Thus, all mature soils developed on smooth, flat, or gently sloping surfaces and existing for a long time undisturbed by erosion or deposit or by the activities of man owe their essential characters not to

the kind of rock from which they originated but to the nature of the climate in which they develop.[521] Hence, all stable, mature soils of a given climatic region belong to a climatic soil type. They tend to show a similar sequence of horizontal layers, irrespective of the underlying rock, the latter causing only minor differences. These horizontal layers constitute the soil profile, which, in turn, has a profound effect upon the water, air, and nutrient relations of the soil and, consequently, upon root extent and distribution. The parallel development of soils and vegetation and the rôle of the two in helping determine one another are of great interest and importance.

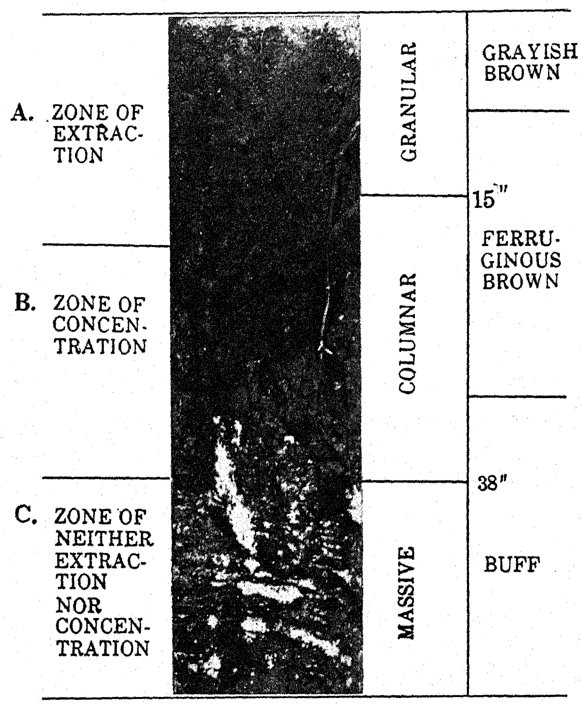

FIG. 102.—Soil profile of a mature upland silt loam in eastern Nebraska.

Soil Profile.—Most soils consist of particles of various sizes, chemical constitution, and degree of solubility. During the long periods of time, calcium carbonate and other soluble materials are leached from the surface soils and carried down to lower layers. The finer, insoluble soil particles (colloidal clay, etc.) are also mechanically carried downward to variable depths which depend largely upon the amount of rainfall and the rapidity with which the water is absorbed and transpired by the vegetation. Thus, the surface layers of a mature soil are poorer in soluble salts as a result of leaching and coarser grained because of eluviation or washing down of the colloidal clay. These layers constitute *A*, the *zone of*

extraction. The soil immediately below this zone and into which the soluble salts and the finest soil particles have been carried is designated as B, the *zone of concentration.* Obviously, at greater depths there is a third zone C, where neither extraction nor accumulation has occurred.

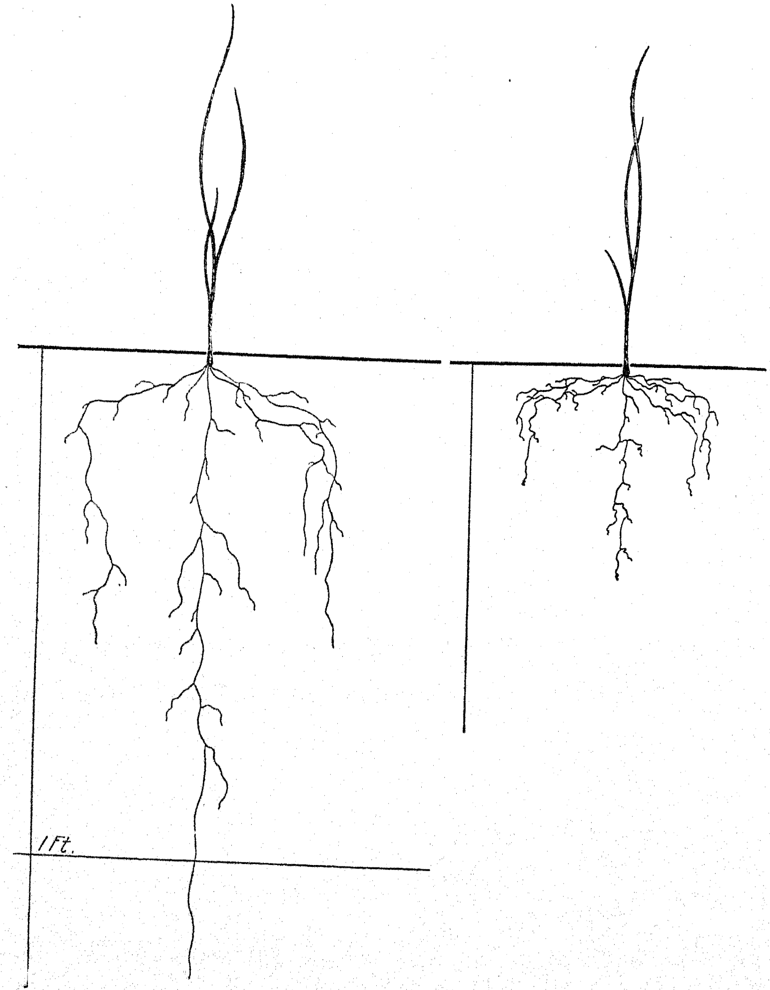

FIG. 103.—Onion seedlings of the same age. The one on the right was grown in compact soil, the left in loose soil. Both drawings are made to the same scale.

The following example from an upland prairie soil in eastern Nebraska illustrates characteristics considered in describing soil profiles:

As a result of the processes of development, the mellow, surface soil has a *granular structure* (Fig. 102). This layer has lost much of its colloidal clay. The forces of weathering, especially repeated freezing and thawing and alternate wetting and drying, together with the greater

humus content and the favorable effects of root activities, have all combined to produce this excellent granular structure. It is distinctly different from that below, which has a higher clay content and which clearly shows a *columnar structure*. Here, due to alternate wetting and drying, the tenacious clay, from which the lime has been leached, has formed irregular columns the surfaces of which are much more weathered, darker in color, and richer in nutrients, than the interior.

In the granular layer, roots penetrate easily and spread widely, thoroughly ramifying the soil. This soil layer has the greatest supply of roots, certain dominant grasses and a few other species scarcely penetrating more deeply. Penetration is much more difficult and branching

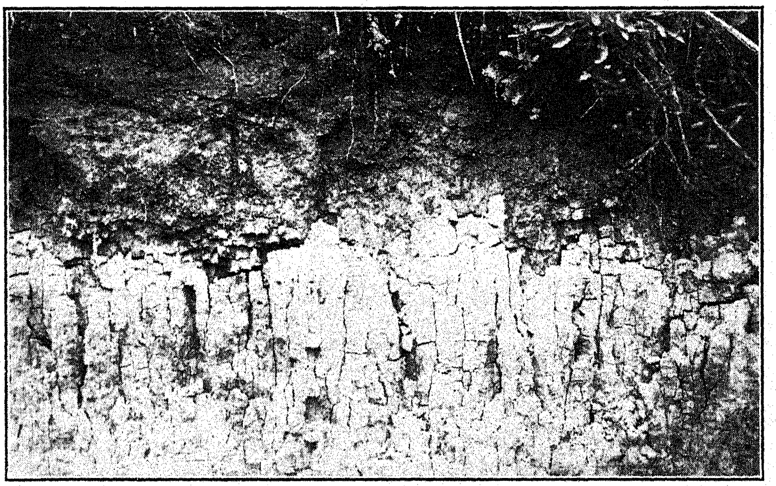

FIG. 104.—Soil profile on low, flat, forested silt loam soil. The columnar form is typical of the B horizon of mature soils of southern Illinois developed under poor drainage. (*After Norton and Smith.*)

less pronounced in the columnar layer. Here the rootlets are found almost entirely appressed to the surfaces of the columns, where water penetrates most readily, air is most abundant, and nutrients apparently more concentrated. Relatively few penetrate the interior of the columns. When they enter the *massive* layer below, they assume a more normal branching habit and are much more easily excavated, since clay is less abundant and the lime occurs in such amounts as to give the soil a mellow structure. Since there is less clay, the soil expands and contracts less upon wetting and drying.

The texture of zones *A* and *B* is due to the processes of soil development, that of *C* is due to the character of the parent rock and the degree of its decomposition.

The color of the soil changes with depth as does also its consistency, that is, its plasticity, friability, and compaction. Maximum compaction,

for example, occurs in Fig. 102 in the columnar layer where the soil is very hard when dry. Soil structure and consistency have a marked effect on the water, air, and nutrient relations. These factors, with mechanical resistance to penetration, profoundly affect the root habit (Fig. 103). The application of a few drops of weak hydrochloric acid shows that the lime has been leached to a depth of about 35 inches, a point indicated by a mealy appearance of the soil. The soft, chalk-like deposits of calcium carbonate show plainly at greater depths and a few streaks occur above 35 inches (Fig. 104).

To Examine Soil Profiles.—Remove the exposed surface of weathered soil from a steep bank along a railway or road by means of spade or pick. Examine the several horizons of which the soil profile is composed. How deeply do the roots penetrate? Where are they most numerous? What is the depth of greatest compaction? Note and explain the changes in color from surface to subsoil. How do the different horizons vary in consistency? Place a small amount of soil on a watch glass and moisten with distilled water. Add a few drops of concentrated hydrochloric acid. Note the degree of effervescence. A very faint effervescence can be heard more easily than seen. If there is none the soil is acid. Test each of the several horizons and determine at what depth lime accumulation occurs. Compare this soil profile with one in lowland.

Climatic Soil Types.—Soils that are young, *i.e.* recently derived from rock or built up by deposit due to wind or water, as well as badly eroded soils, do not show a profile similar to that of mature soils upon which climate and vegetation have acted and reacted for long periods of time. The character of the climate eventually alters the nature of the soil from nearly all kinds of rock to such an extent that the mature soil type is similar in its main features throughout a given climatic region.

The soils of the Great Plains, for example, consist of three great belts extending quite across the United States from Canada to the Gulf of Mexico.[332] These correspond, in general, to differences in degree of grassland climate and in the type of vegetative cover. All of the soils (from near the Rocky Mountains eastward to about the one hundredth meridian), when mature, are dark in color and underlaid by a zone of lime-carbonate accumulation, beyond which water usually does not penetrate. They differ, however, in degree of darkness of soil color and depth of the carbonate layer. Where precipitation is least, the soil is brown and the carbonates have accumulated at depths of only 12 to 18 inches. This delimits the area in which water and nutrients are absorbed by the short-grass vegetation. The effect of vegetation upon the profile is shown by its removal. Where land is broken, water penetrates quite beyond the carbonate layer. Had there been no vegetation to absorb the water, the layer of carbonate accumulation would probably never have developed.[464]

Where precipitation increases eastward, the carbonate layer is deeper, vegetation is more abundant and taller, and the soil of a dark

brown color. Still farther eastward the carbonate accumulations usually reach depths of 5 or 6 feet. The soil is black in color and continues dark to a greater depth (8 to 24 inches) than in any other part of this climatic region. The vegetation is of the deeply rooted, mostly mixed-prairie type.

Another climatic soil type is represented under a heavier rainfall eastward (prairie soils) where the soils are black or brown in color and are completely leached of rock carbonates, which do not accumulate at a lower level. In this climatic type the soil is moist to a depth of many feet, in fact, often to the underlying water table. Roots of native plants penetrate very deeply (6 to 20 feet) and tall-grass climax and subclimax prairie prevail.

Quite in contrast is the soil of the climatic type in parts of the New England states where a surface layer of raw humus often 4 to 5 inches deep is underlaid with a few inches of a leached grayish soil, below which the thin, reddish brown, glacial soil soon gives way to the parent rock. The absorbing roots of coniferous trees are often largely confined to the surface layer of raw humus or duff.[359] A pronounced effect upon such a soil profile may be brought about, sometimes within only a score of years, by converting the coniferous forest into stands of hardwoods.[162,357a]

WATER CONTENT

Water content exerts a much greater influence than any other factor upon the form and structure of a plant. Likewise, the most important differences between habitats are due to differences of water content. Water is important to the plant in many ways. It is a component of protoplasm and, with carbon dioxide, is essential in building plant foods. It usually constitutes 70 to 90 per cent of the weight of herbaceous plants. All substances that enter plants must do so in solution. Water is the great solvent. It serves as a medium of transport of food materials and foods from place to place, since their transport can take place, for the most part, only in solution. It keeps the cells turgid or stretched, a condition essential for their normal functioning. It also serves to prevent excessive heating of the plant, acting as a buffer in absorbing the heat generated by the multitudinous chemical reactions taking place in the plant. A large quantity of heat energy is absorbed when liquid water is changed into the vapor form during transpiration. In corn for example, a transpiring leaf is uniformly cooler than a dead one. A difference of 8.5°F. has been found in the sun when transpiration was high, and 4.2° at the same time in the shade.[280] The greatest sources of danger which the plant has to meet are insufficient absorption and excessive transpiration.

Kinds of Soil Water.—After a heavy rain or irrigation, much of the water drains or sinks away. This is called *gravitational water*. But large

amounts are retained in the minute spaces between the fine soil particles, as films surrounding the particles, and by adsorption by the soil colloids. Not all of this water is available to the plant. Even air-dry soil contains appreciable amounts of water, as may be shown by heating dust in a closed container, when drops of water will be deposited on the lid. The relatively small amount of water absorbed by dry soil from the atmosphere is termed the *hygroscopic water*. It is held so tenaciously by the soil colloids which coat the rock particles that it is unavailable to plants.

The *hygroscopic coefficient* is a term used to designate the maximum hygroscopic water that a soil will hold, *i.e.* the percentage of water absorbed by a dry soil from a saturated atmosphere. Since it is unavailable for plant growth, it is usually subtracted from the actual water content of the soil to obtain the available water content.

The total amount of water that is held against the force of gravity and the downward pull of capillarity and does not drain through the soil is termed the *water-retaining capacity*. It is expressed in percentage of the dry weight of the soil. It includes the hygroscopic water as well as the much larger quantity that the soil holds besides, commonly called *capillary water*. The amount varies considerably in different soils; a coarse sand under field conditions may retain only 12 per cent of its dry weight of water, but a silt loam may retain 35 per cent. The smaller the particles of a soil the more film surface it will present for the retention of water. Likewise, the greater the proportion of colloidal constituents, clay and humus, the more water there will be held. The high absorptive power of soil colloids for water is due to the extremely large surface exposed by matter in the colloidal state. The field water-retaining capacity of sandy soil is increased about 5 per cent with an increase in organic matter of 1 per cent.

Water-retaining Power.—The water-retaining power of the soil is determined by a number of factors. Most important among these are soil texture or size of particles, soil structure, *i.e.* the arrangement and compactness of the particles, and the amount of organic matter. Since water is held as thin films upon the surface of the soil particles, and runs together forming drops and masses only in saturated soil, the amount necessarily increases with an increase in the water-holding surface. The latter increases as the particles become finer and more numerous and thus produce a greater aggregate surface.

To Determine the Maximum Water Capacity of a Soil.—Cut a circle of filter paper to fit the Hilgard maximum-water-capacity pans, moisten, and adjust smoothly. Fill with dry soil, using one sample of sand and one of potting loam, tapping on the edge of the pan a few times, and level the surface. Place the cup in a tray containing water that comes up about 1 millimeter on the side. Add water, if necessary, to retain it at this level. At the end of 30 minutes, remove the pan from the tray and let drain for 4 minutes. Wipe off any adhering water. Quickly pour the soil that does not adhere to the filter paper into a soil can, cover and weigh. After driving off

the water by placing in the oven at 110°C. for 24 to 48 hours, reweigh and determine the maximum water capacity. This method gives results much higher than the field water capacity.

To determine the latter, use a heavy galvanized-iron cylinder 3 or 4 inches in diameter and 6 inches long with a perforated bottom. Invert the cylinder and drive it into the soil until the bottom is even with the surface. Dig up and cut the soil core off evenly with the top. Stand it in water 4 inches deep for a day. Drain for an hour, wipe dry, and weigh. Reweigh after the soil has been thoroughly dried at 110°C. and calculate the total amount of water held by the soil.

The movement of water upward or downward in a soil is likewise dependent upon the size of the particles. As the latter become finer, tne irregular capillary spaces between them grow smaller and the upward or capillary movement is increased. Thus, the surface layers of silt loam or clay soils in contact with the water table at a depth of a few feet may be quite moist, while those of a coarse-grained sand would be dry as far as the capillary rise of water is concerned. On the contrary, the downward movement of water, *i.e.* percolation caused by gravity, is retarded by a decrease in the size of the soil grains and hastened by an increase. Thus, both capillarity and porosity are dependent upon the texture of the soil, though in a manner directly opposite to each other.

The effect of structure on water-retaining power is shown by the fact that a soil in good tilth will hold more water than a hard, compact one. Clay soils, especially when poor in lime, hold water tenaciously and retard or prevent its movement. They are liable to become water-logged, preventing the ingress of air. The presence of calcium carbonate greatly improves the structure of such a soil by flocculating the colloidal particles and causing them to act as larger units. The clay becomes more porous, holds less water, and is a much better environment for roots because of better aeration, greater mellowness, and less shrinking and cracking upon drying.

Organic matter affects water content directly by retaining water in large amounts on the extensive surfaces of its colloidal constituents and holding it like a sponge in its less decayed portions. It also has an indirect effect through soil structure. Sand particles are loosely cemented together by it; hence, percolation is decreased, and water-retaining capacity increased. Minute clay particles are enclosed in aggregates by the colloidal film of humus. This results in increased percolation and a decrease of the aggregate soil surface for retaining water by capillarity.

To Ascertain the Effect of Humus on Water-retaining Power.—Repeat the preceding experiment (Hilgard method) after having mixed with the sandy soil 5 per cent by weight of thoroughly decomposed organic matter, such as forest leaf mold.

Available and Non-available Water.—If a rooted plant is allowed to wilt and die, an examination of the soil shows that some water still remains. The amount depends upon the kind of soil. It is small in

coarse-grained sand, sometimes less than 1 per cent. In silt loam or clay, it may amount to 20 per cent or more. But all soils are alike in retaining some portion of the water content. This is due to the fact that the attraction for water of the colloidal-coated soil particles increases as the films grow thinner, until, finally, they do not furnish water to the plant rapidly enough to keep it from wilting and subsequent death. Experiments indicate that the absorbing power of the plant, in terms of osmotic pressure, may be greater than the force with which the films of water are held about the soil particles. Unless the soil is quite moist and the water films relatively thick, capillary movement is very slow, and when the root hairs exhaust the water from the particles with which they are in contact, the plant wilts. This water relation is illustrated by the fact that seeds placed in a dry soil may swell slightly but not enough to germinate. But if they are moved about in the same soil or new soil particles continually brought in contact with them, germination takes place.[489]

The water retained in the soil at the time of permanent wilting is called the non-available water or *echard* (to withold). It is usually but a small part of the water commonly present, particularly in moist or saturated soil. Of the total water content or *holard* (whole amount), the larger portion can be absorbed by the plant and is consequently termed available water. The response of the plant is determined by the available water and not by the total amount present. Obviously, the available water or *chresard* (amount for use) differs for different soils.

The echard is not determined entirely by the type of soil, since some plants can absorb more water from a given soil than others. In spite of extensive experiments with a wide range of soils and plants, this phenomenon needs further study. Certain investigators have concluded that species differ only slightly in a given soil as regards the water content when permanent wilting occurs. The water left in the soil at this time has been termed the *wilting coefficient.* Taking 100 to represent the average wilting coefficient of the numerous species tested, an extreme range from 92 to 106 was found.[52] Among most of the plants, differences were even less and the conclusion was reached that they were so slight as to be without practical significance in the selection of crops for growth in semiarid regions. The differences were not believed to be due to a greater attractive force exerted upon the soil moisture by the various species but to differences in root distribution.

The root hairs of any plant are in contact with only a portion of the soil particles and when the soil becomes dry the capillary movement of water is very slow indeed. The rate at which plant roots can develop in the soil and reach new supplies is probably extremely important. It seems probable that plants with extensively branched root systems, abundantly furnished with root hairs, and thus coming in contact with

the largest possible soil surface, and with aerial parts morphologically and physiologically adapted to conserve water, would reduce the water content of the soil mass to a minimum before wilting. Conversely, it would seem that plants with relatively scanty root development and tops poorly adapted for water conservation would leave a greater water residue at the time of wilting. Sorghum, for example, is much better adapted to semi-arid regions than is corn. A study of the cause of this difference revealed the fact that both species possessed, at any period of growth, the same number of main fibrous roots and that the general extent of the roots in both a horizontal and a vertical direction was the same, *i.e.* 3 to 4 feet on all sides of mature plants, and 6 feet deep. The length of the secondary roots was also found to be approximately the same. But both primary and secondary roots of the sorghums were more fibrous than those of corn and the secondary roots were twice as numerous. This root system, moreover, which, judging from the number of secondary roots, would be twice as efficient in the absorption of water, supplied a leaf area which was approximately only half as great as that of corn. Although sorghums also have other characteristics enabling them to endure drought, the thorough manner in which their roots ramify the soil for water is of fundamental importance.[352]

The exact permanent wilting point is difficult to determine in many plants, and permanent wilting should not be confused with temporary wilting from which the plant recovers. A plant is permanently wilted only when it will not regain turgidity when exposed to a saturated atmosphere. It is most easily determined with large-leaved herbaceous species which readily show wilting. With rigid-leaved plants, as yucca, or leafless ones with succulent stems, like cacti, special methods (*e.g.* balancing the plant) are necessary to determine the point when transpiration exceeds absorption. Several investigations point to the conclusion that the water content at the time of permanent wilting is not a constant but changes with the environmental conditions under which the plant is grown.[69]

Determining Non-available Water.—In order to find the amount of water non-available for a plant in its own habitat, it is necessary to produce wilting by cutting off the water supply. This may be done by digging up a plant and transferring it to a container of large size. The soil must be protected both from the loss of water by evaporation and from the intake of moisture resulting from rain. Since the roots of most plants are very deep or spread widely, they are almost sure to be injured by such a procedure. It is much simpler to start the plant from seed or vegetatively under controlled conditions.

The soil mass should be very uniform throughout and not stratified or otherwise irregular in texture. It should be brought to a uniform water content before placing it in the container, otherwise it is very

difficult to moisten it uniformly. Small volumes of soil might remain quite dry and thus introduce an error into the final moisture determination. The surface or sides of the soil mass should not be allowed to lose water except through root absorption, otherwise they may become drier than the non-available point before the water in the central mass has been greatly reduced. Sudden fluctuations in temperature should also be avoided, otherwise water may distill from the soil and condense on the inner walls of the container as a result of differences in temperature. Thus, water may be made available for absorption which the roots otherwise might not be able to secure.[52]

To Determine the Amount of Water Non-available for Growth.—Mix thoroughly a quantity of screened potting soil, adding enough water from a sprinkler to bring it to an optimum water content. In the same way, prepare another lot consisting of one-third potting soil and two-thirds sand. Cover each lot and let it stand for 24 hours. Fill 4, glazed, gallon jars, two with each kind of soil, compacting the soil rather firmly. Plant seeds of corn, sunflower, or wheat, soaked for 4 hours, about an inch deep, and then cover the soil with an inch of dry sand to retard surface evaporation. Place the jars in much larger ones or in a large box and fill the interspaces with moist soil so as to maintain soil temperatures which fluctuate slowly and are as nearly uniform as possible. After a few weeks, when the plants have wilted so that they will not recover even when placed in a saturated atmosphere under a bell jar, remove the sand mulch and the surface inch of soil. Mix the remaining soil, which is thoroughly ramified by roots, and determine the water content of duplicate samples from each jar. If two kinds of plants are grown in one container, the relative time of wilting of each may be determined. Save samples of the soil for the experiment below.

In field practice it has been found that the hygroscopic coefficient of the soil, which is a function of texture, gives a fairly close approximation of the amount of water left in the soil at the time of wilting.[10] Since the root systems of plants in nature often ramify many cubic feet of soil and extend to great depths, the advantage of an indirect approximation of the non-available water at the different soil levels is obvious. Representative samples of soils are easily secured, air dried, and the amount of water they will absorb from a saturated atmosphere when exposed in thin layers at a constant temperature determined. This is the hygroscopic coefficient.

To Determine the Hygroscopic Coefficient of a Soil.—Use a box 12 inches long, 10 inches wide, and 10 inches deep. It should be made of wood an inch in thickness and lid and walls should be lined with blotting paper which extends downward into a tin pan filled with water occupying the bottom of the box. Two copper or aluminum trays 5 by 7 inches and ¾ inch deep are held on a shelf of woven wire 6 inches from the bottom of the box. The inner walls of the box are thoroughly saturated with water and the box is kept in a room of approximately constant temperature, *i.e.* 25° or 30°C. Sprinkle approximately 10 grams of air-dry soil evenly over the bottom of the tray and cover the box. After 24 hours, pour it on to a sheet of glazed paper and then immediately into a weighing bottle. After weighing, dry at 110°C., reweigh, and calculate the amount of water lost. Samples are always determined in duplicate

in separate boxes and checked against a soil of known hygroscopic coefficient run at the same time.

Determining Available Water.—Water content is one of the most important habitat factors, and an intimate knowledge of water relations is fundamental to the understanding of plant behavior and distribution of vegetation. In obtaining samples of soil for finding water content, a spade or trowel may be employed for securing shallow samples, but this method has the disadvantage of seriously disturbing the vegetation. In all cases, representative cores of soil should be obtained from the several depths to which the roots penetrate and in which they are absorbing. In stony and gravelly soils this is a difficult procedure, but elsewhere it is easily accomplished with practically no disturbance of the plant cover by use of a soil tube or geotome (earth cutter). This has a

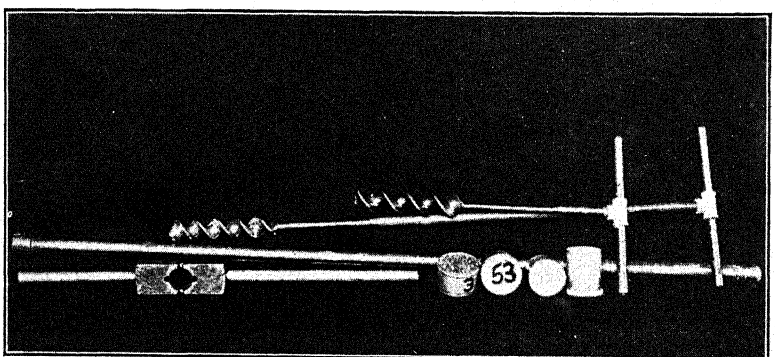

FIG. 105.—Types of soil tubes or geotomes. These are made in various lengths. With the longest one shown here, samples may be secured to a depth of 4 feet.

sharp cutting edge on one end, contracted to a slightly smaller diameter than the bore of the tube, and a reinforcement on the other end, to allow pounding into the soil (Fig. 105).

The practice is to remove the vegetation from a square inch and sink the geotome to a depth of 6 inches. The soil is then emptied, by inverting the geotome, into a seamless metal can with a closely fitting friction or screw-cap lid. A second sample is taken at a distance of a foot from the first, and a third, if necessary, to secure enough soil nearly to fill the container, which should hold at least 200 grams of moist soil. Using the same holes, samples of the second 6-inch soil layer are secured. The cans are numbered in large figures on both side and lid. If the first can is inverted after filling and the others placed in a row in sequence of depth, there is no possibility of confusion. Samples below the first foot are secured in foot sections. Only one of the holes need be used, since the soil core is sufficiently large for a sample. Samples are always taken in duplicate, the second lot at a distance of a few feet from the first.

This tends to equalize differences in soil texture, etc., and affords a reading in case one sample in the series is accidentally spilled. When the sampling is completed, a record should be made of the containers in the manner indicated in Table 5, and water-content determinations made in the laboratory.

TABLE 5.—WATER CONTENT OF SOILS AT VARIOUS DEPTHS

Station and date

Depth of sample	Can number	Wet weight, grams	Dry weight, grams	Can weight, grams	Per cent water	Average per cent water
0 to 6 inches	36	208.2	185.4	53.5	17.2	17.4
0 to 6 inches	42	205.8	182.6	50.8	17.6	
6 to 12 inches	21	192.5	165.1	51.1	24.0	24.1
6 to 12 inches	13	209.1	178.1	50.2	24.2	
1 to 2 feet	4	229.5	193.1	51.6	25.7	25.4
1 to 2 feet	11	228.7	192.8	50.0	25.1	

The soil cans should be weighed to the nearest tenth-gram soon after the sample is taken, although, if necessary, they may be kept for several days without appreciable error. After determining the wet weight (including soil, can, and water), the lids are removed and placed with the cans in an oven kept at a temperature of 110°C. The dry weight (soil and can) is next determined, after one or several days, when the soil ceases to lose weight. Much more time is required to drive off the water from clays than from light-textured soils. Finally, the weight of the can and lid is determined. Since their weight remains fairly constant, this need be done only about twice each season. Water content is expressed in percentage of the dry weight of the soil. Thus, in making the calculation, the can weight is subtracted from the dry weight (dry soil and can) and the difference between the wet and dry weights (loss of water) divided by this number. From the percentages thus obtained, the non-available water, previously determined, should be subtracted.

Time and Place of Sampling.—Since the water content at depths greater than 2 feet usually changes rather slowly, it is not necessary to secure samples so frequently here as from the surface soil. In field practice it is usual to determine water content in the surface layers weekly, and during periods of stress at even more frequent intervals. The total amount of vegetation which can exist on a given area is usually determined by the amount of moisture available at critical times. Under ordinary conditions, the time of day at which samples are taken is of little importance, since the variation during a day is usually slight. This, of course, does not apply to soils that have just been wetted by rain or

irrigation. In determining the location of readings in the field, it is desirable to obtain a range as great as possible. Differences in water content are invariably indicated by differences in the kind and development of vegetation. A series of stations on the crest, mid-slope, and base of a steep hill will show this correlation. The exact location of each station should be noted so that future readings may be made in the same place. Samples should not be taken, of course, in too close proximity to holes left in former samplings.

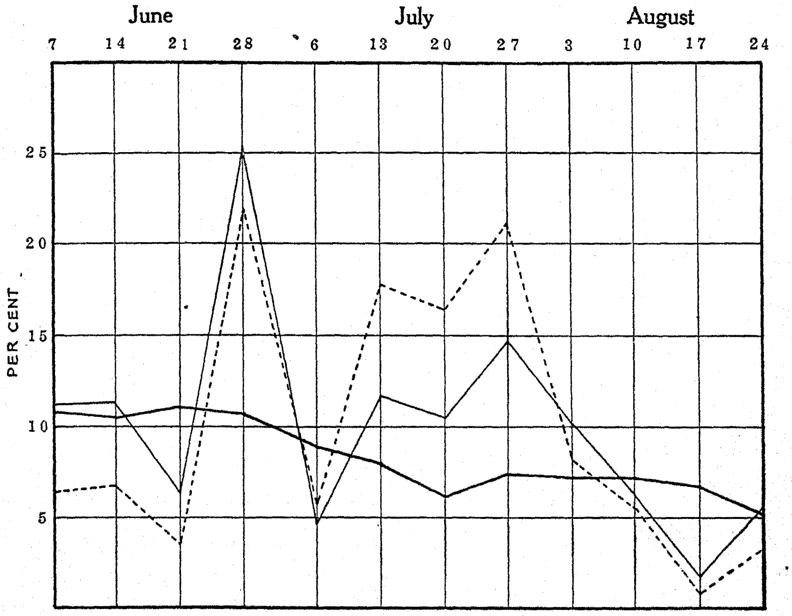

Fig. 106.—Available water content in prairie at Lincoln, Nebraska, during 1922; broken line at 0 to 6 inches depth; light solid line at 6 to 12 inches; and heavy solid line, where fluctuation is least, at 12 to 24 inches.

Various stages in the development of a sere should be studied in relation to their water content, and, if possible, weekly comparison made between the water content of such vegetational units as woodland, grassland, marsh, etc. Even small differences in slope, exposure, or topography frequently cause marked differences in water content. A slight depression, such as that worn by wheels in an old road, where water runs in, may have 5 to 10 per cent more moisture than the adjacent ridge from which run-off occurs. Minute differences in the structure of vegetation may often be explained by a determination of water content.

To Determine Water Content.—Select representative stations in two or more habitats and determine the water content each week. Show the results by means of graphs. The stations should also be used for the determination of other habitat factors. Also, determine the water content in different places in the same kind of

vegetation, *e.g.* forest, grassland, etc., and try to account for variations in kind and density of dominants. In a similar manner, study zones about ponds, etc. Give the reasons for the differences between the various stations. To what extent and in what ways are these reflected by the plants?

Interpretation of Data.—It can not be too strongly emphasized that the measuring of the factors of the habitat is of little value unless the data thus secured are studied in relation to plant activities. The water available to the plant at the several depths at different times may readily be compared if the data are plotted in the form of a graph as shown in Fig. 106. This method is also useful in comparing the water relations of different communities (Fig. 107).

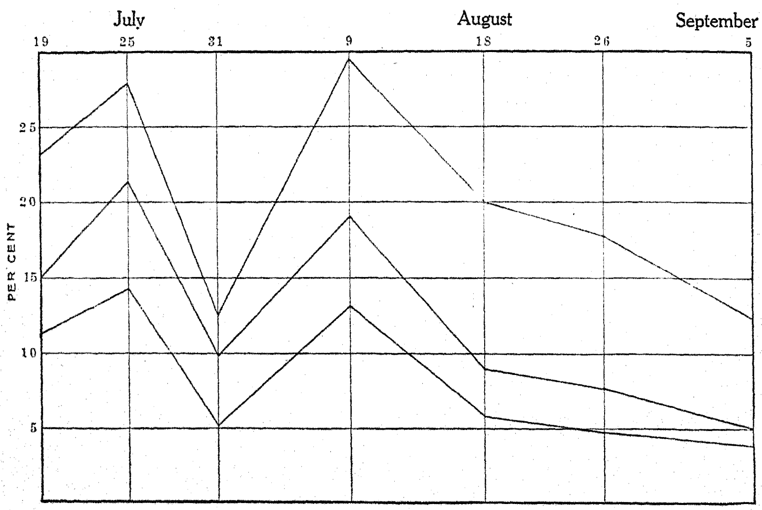

FIG. 107.—Available water content at a depth of 0 to 6 inches in three forest communities in southeastern Nebraska during 1917. Upper line, linden; middle, red oak; lower, bur oak.

FACTORS MODIFYING WATER CONTENT

Water content of soil is directly or indirectly dependent upon precipitation. The indirect topographic factors, moreover, such as slope, surface, etc., largely determine the amount of run-off and thus greatly influence water content. Likewise, temperature and evaporation have a marked effect upon the rate of water loss from the soil surface. Each of these factors will be considered in so far as they affect the water content of the soil.

Precipitation.—In all habitats except those where the supply of water is constant owing to the presence of springs, streams, ponds, or other bodies of water, the dependence of water content upon precipitation is absolute. Cover, kind and structure of soil, and slope determine how much of the latter finds its way into the ground, but their action is

secondary. Daily rains are able to keep practically any soil moist, regardless of its character or the slope. All habitats not covered with water reach their maximum water content after a heavy rain or during a rainy season. The water decreases gradually throughout a dry period or season, only again to approach the maximum when precipitation takes place.

Precipitation occurs in various forms, such as rain, hail, dew, frost, and snow. Of all these, rain is by far the most important. Except locally, hail is too infrequent to be taken into account. Frosts have, at best, only a slight and fleeting effect upon water content, especially in view of the fact that they usually occur outside the growing season.

Snowfall is often of great importance. It not only acts as a cover to prevent evaporation but upon thawing it also enters the soil directly just as rain does. The rapid development of spring vegetation in climates where snow accumulation is great is largely determined by the water supply from the melting snow. Because of drifting, due to wind, protected hillsides, ravines, etc., are often better watered than exposed sites. The loss by run-off from slopes is much greater, owing to the frozen condition of the soil.

Dew is almost always too small in amount and too fleeting in temperate climates to add directly to the water content of the soil. By its own evaporation it increases humidity and thus decreases slightly the amount of water lost by evaporation from the soil and by bedewed plants. In certain tropical desert regions, such as those of North Africa, dew is of considerable importance. During the late winter and early spring, it provides most of the surface water upon which the ephemeral annuals live, rainfall being extremely light. It is deposited in large amounts owing to the greater moisture of the air at this time of year and the strong radiation of heat at night which cools the surface of the desert. In studying the water content of most habitats, however, a knowledge of rainfall will suffice.

Measurement of Rainfall.—Rainfall is measured by means of a rain gage, an instrument which collects in a narrow vessel the rain falling upon a large surface.[283] In the standard gage, the ratio of surface between receiver and tube is 10:1. A direct measure of the water in the tube must be divided by 10 to give the rainfall, or a standard measuring rod, upon which this compensation is already made, may be used. The purpose of the smaller, inner tube is to increase the depth of the water and permit of more accurate reading. Readings may be made to 0.01 inch. After a heavy rainfall, when the water from the inner tube has overflowed into the outer one, first the inner tube is read, emptied, and then the water from the outer one poured into it and the amount recorded. Where rain gages are not available, it is fairly satisfactory to use the reports of rainfall obtained from a neighboring weather station when the latter is not more than a few

miles distant, except in mountainous regions or others with very irregular topography. But even in level countries, marked differences in rainfall, caused by local showers, may occur. The effect of rainfall upon water content is best ascertained by taking soil samples in different habitats immediately after a rain and then determining the increase in water content.

Relation between Precipitation and Water Content.—Only a very general relation exists between the total amount of precipitation and the water content of soil. Many factors intervene to decrease the effectiveness of the rainfall in increasing water content about the roots of plants. Much of the water may be intercepted by the crowns of plants and evaporate again without reaching the soil surface. The rains may fall in such light showers as to have little influence upon wetting the soil. Conversely, it may be of such a torrential nature that only part of it can be absorbed and the rest is lost as run-off. Where temperatures are high and humidity low, much water is lost directly from the soil by evaporation and the efficiency of the rainfall thereby greatly decreased. These losses are modified by slope, surface, and the cover of vegetation.

To Determine the Depth of Water Penetration.—After a heavy rain following a dry period, examine the soil in a plowed field, hard bare area, grassland, woodland, etc., and determine the depth of water penetration. What is the relation between this and the plant cover?

Rainfall Interception.—It is a matter of common observation that even isolated plants, especially trees and shrubs, intercept much rain. The soil surface below the plants may remain dry during light showers, while that not protected is rather thoroughly wet. Extended experiments have shown that much water is held as thin films on the upper surfaces of the leaves or as drops or blotches or retained in capillary depressions such as those adjacent to veins. Large quantities also accumulate on the surfaces and in the crevices of the bark of trunk and branches from which it evaporates.[248] The amount of water thus retained is reduced by the wind, but the rate of evaporation is increased.

Rain gages placed in bur oak and linden forests in eastern Nebraska received 16 and 28 per cent less water, respectively, from a total precipitation of 14 inches during 3 summer months than a similar gage just outside the forest. The mean interception loss under 11 different species of trees in New York was about 40 per cent of the total rainfall. The amount of water lost to the soil in this manner varied from 70 to 100 per cent in light showers and was about 25 per cent in heavy, long-continued rains. In these experiments, the water running down the trunks of the trees was caught and measured, and this was not included in the amount intercepted. Needle-leaved trees intercept more water than broad-leaved ones. In winter, interception by deciduous trees is 50 per

cent of that of summer. Interception losses from fully grown crops of rye, red clover, etc., are only slightly less than those due to trees, but of course this effect is only of short duration.[248] Thus, it seems that wherever vegetation covers the earth, it intercepts a part of the precipitation and diminishes the water supply. Exceptions occur in certain cases, especially where the moisture is precipitated as a fine mist. In South Africa, for example, a condensation gain of 80 to more than 1,000 per cent has been experimentally determined where large amounts of moisture are deposited upon the exposed crowns of forest trees and scrub.[332a] The forests may be dripping wet, while the ground immediately beyond their margins is comparatively dry.[390] More study is needed in this important and interesting field.

To Measure Rainfall Interception.—Secure two or more of the small type of rain gages (diameter 3 inches) or substitute straight-walled vessels of equal cross-sectional area such as ½-gal., glazed jars. Place them under various types of vegetation such as forest, scrub, etc., or under isolated trees and bushes, maintaining a control in the open. After each rain or shower, measure the amount of water in each by pouring it into a graduate. Calculate the percentage intercepted.

Manner and Time of Precipitation.—The influence that a rain exerts in replenishing the soil water is not in proportion to its amount. Light rains falling on a warm, dry soil are totally converted into vapor within a few hours and have no effect upon the water content. Heavy rains are often of such short duration that run-off is very great and a relatively small amount of water enters the soil. Rainfall in deserts consists largely of these two types and they are also very common in semiarid regions. Where a shower furnishes only 0.15 inch of rainfall, it is of no value in increasing water content.[481] Not infrequently, a monthly precipitation of 2 or 3 inches is distributed in so many light showers that it has little or no effect upon water content.

The seasonal distribution of rainfall also has a marked effect upon water content and, hence, upon the type of vegetation the latter will support. This is especially true in climates where there is a winter resting period. The great prairie and steppe regions of the temperate zones, for example, have their rainfall chiefly in early summer. Thus, the surface soil is kept moist and the grasses growing during their vegetative season. This is illustrated in varying degrees in the North American grasslands. Where rainfall is fairly abundant and occurs throughout the growing season, a mixture of both early- and late-blooming grasses, etc., are found. Where it is scanty and intermittent, the dominant grasses require only a few weeks to flower and seed. Over the greater portion of the Great Plains, the average annual precipitation is enough to insure the production of crops, but the uncertainty of the distribution of the rainfall makes crop production hazardous.[82]

The amount of water lost in run-off depends primarily upon the manner of precipitation but also, in a large measure, upon the kind of cover, soil, and slope. Run-off is usually greatest where sudden heavy showers or rainstorms lasting for only a short time fall upon bare slopes or sparse or low-growing vegetation. The dry soil surface, poorly protected by a cover of plants, will not rapidly absorb water and especially if the soil is low in humus content and of fine, compact texture. Even on relatively level soils, such, for example, as those of the Great Plains, the water lost by surface run-off varies from 15 per cent in light showers to more than 50 per cent in torrential ones.[461] That run-off is great is shown by the large number of dry, sand-choked creeks and swales throughout the region. A continuous shower with gentle rainfall of long duration and with the necessarily high accompanying humidity would be many times as efficient. Where the soil is sandy, run-off is greatly reduced.

Run-off is small in forests. The force of the rain is broken by the trees, the undergrowth, and the forest litter, so that the water does not beat upon the soil. Much of the precipitation reaches the earth by running down the twigs and branches. The mat of duff and humus, which in thrifty, unburned forest is often a few inches thick, absorbs several times its own weight of water like a huge sponge and when filled slowly passes it on to the mellow, mineral soil beneath. From here it seeps out gradually to springs and streams. Such streams furnish the best water supply for the most valuable irrigated lands. Even when the rain is so heavy that the soil is unable to absorb all of the water at once, the excess flows off with no erosion. Streams coming from virgin forests are seldom muddy and are subject to comparatively small variations in flow.[133]

Erosion and Plant Cover.—Decrease in water content and soil fertility and change in soil structure are all closely related to erosion caused by run-off. The latter is greatly influenced by plant cover. Upon areas from which vegetation has been partially or completely removed, the raindrops beat upon the bare soil like millions of little hammers. The soil is compacted and its absorbing capacity is reduced. The excess water accumulates on the surface and in running off removes with it the surface-soil particles, the humus, and the dissolved salts. Whether there is a more or less uniform washing away of the soil over the entire area, as in sheet erosion, or whether it is by the formation of gullies, landslides, or erosion along river bottoms, the results are the same. The remaining plant cover is destroyed, the richest portion of the soil is removed, leaving exposed a hard, compact, poor absorbing surface. Water content is further affected by a lowering of the water table, which results in a constant tendency of the water in the upper layers to sink to a lower level. Soil removed from the uplands causes great

destruction in silting over vegetation of adjoining lowlands and in impeding navigation.[29]

The mantle of soil that clothes the mountains and protects the headwaters of streams acts as a great natural reservoir. It is largely from this source that water for irrigation is obtained. The effectiveness of this natural reservoir is decreased in proportion as the soil is removed or its absorptive capacity decreased by erosion. The gradual release of water through spring-fed streams is replaced by destructive floods. Nearly half the United States—the hilly half—is being seriously impaired by

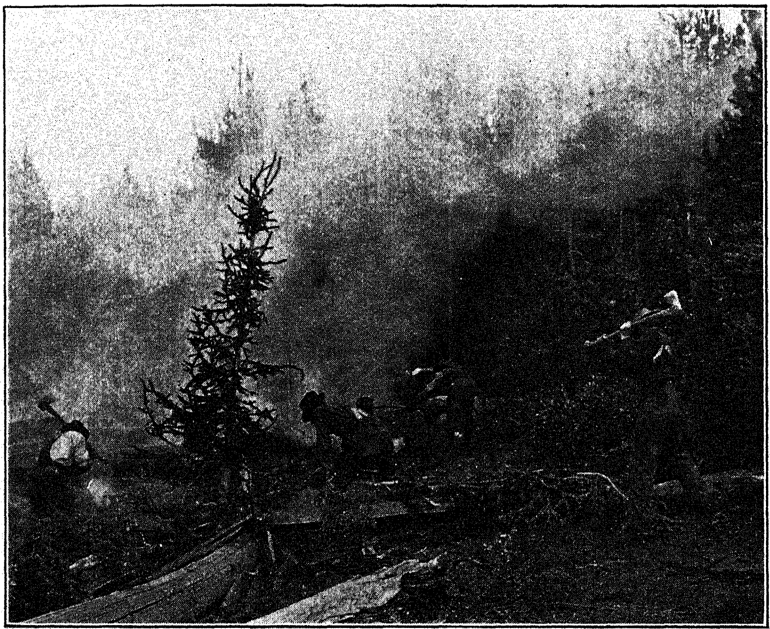

FIG. 108.—Fighting a forest fire. During a recent 5-year period, fire destroyed 56,000,000 acres of forest in the United States, and in many cases exposed the soil to erosion. (*U. S. Forest Service.*)

water erosion. This has been brought about largely by the removal of the natural plant cover, as in the case of clearing forests from nonagricultural land, through destructive lumbering, fires, and overgrazing (Figs. 108 and 109).

Forests, chaparral, grassland, and all kinds of plant cover, living or dead, protect the soil from erosion. This effect is due partly to protection afforded by aboveground parts, in part to the results of humus accumulation, and in no small degree to the binding action of roots and rhizomes. Soil is warmer in winter and cooler in summer under a plant cover and especially in forests and scrub. Hence, snow begins to melt earlier than on exposed ground. Melting proceeds more gradually,

however, since it is retarded by the forest cover after warm weather begins. Thus, the water from the gradually melted snow is more apt to be absorbed, especially since the soil in forests freezes less deeply. Only the removal of the cover of vegetation and subsequent erosion reveals its beneficial effects.[605]

The cutting of the forest cover on a small watershed in Colorado, although in a region of coarse, permeable soil, increased the volume of silt discharge 8.5 times. Within 3 years after the brush cover on a canyon drainage in southern California was destroyed by fire, the soil lost 45 per cent of its water-holding capacity. In Utah, the run-off after

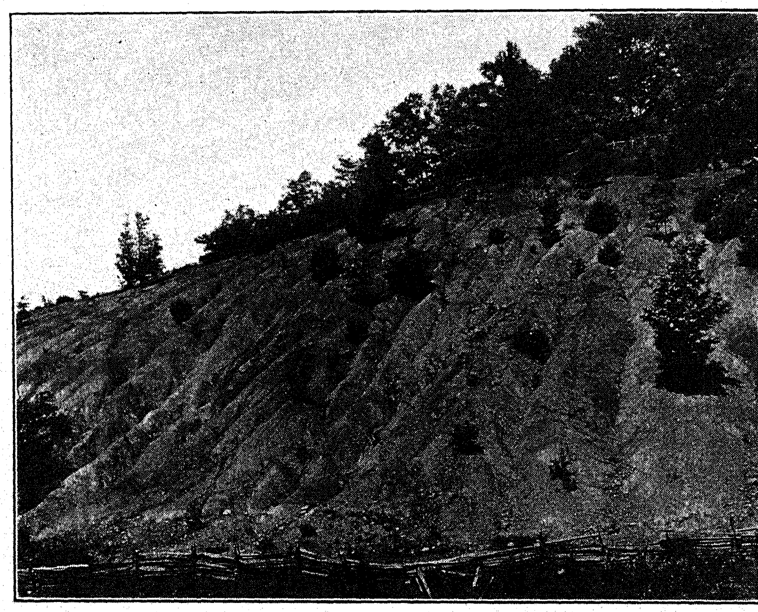

FIG. 109.—View of a mountain slope in North Carolina, after the removal of the forest. In cutting such a forest enough young trees should be left to hold the soil and insure a new lumber crop. (*U. S. Forest Service.*)

rainstorms on overgrazed land was seven times as great as on adjacent areas that were moderately and conservatively grazed.[439] Most of the worn-out lands of the world are in their present condition because much of the surface soil has washed away and not because they have been worn out by cropping.[148] Under cultivation, the rate of erosion is often appalling. Certain Piedmont areas have entirely lost the 8 or 10 inches of top soil within a period of only 30 years. Measurements in Missouri have shown that on a slope of less than 4 per cent, when plowed annually and cropped with corn, the surface soil to a depth of 7 inches is entirely removed in a period of 56 years. The removal of the same thickness of soil in grassland would require thousands of years. Left to herself,

nature brings about an adjustment between erosion losses, soil-forming processes, and the development of vegetation. It is only when man interferes that erosion becomes a seriously destructive force.

Slope and Surface.—In addition to the amount and distribution of rainfall, the type of soil and plant cover, the steepness of slope (topography), and the nature of the surface influence water content. By slope is meant the inclination of the soil surface with respect to the plane of the horizon. The principal effect of slope is in controlling run-off and drainage and, through them, water content. Slope, also, has a less direct influence through its action upon heat and wind, both of which affect humidity, and this, in turn, the rapidity with which water is absorbed or directly evaporated from the surface of the soil. The angle of the slope, moreover, largely determines the amount and type of soil accumulated. It is only on flat ground or gentle slopes that considerable depths of soil accumulate and undergo the characteristic development of mature soil. Slope is expressed in degrees of the angle made by the intersection of a line bounding the surface and the base line in the same plane. It is measured by means of a clinometer, a simple instrument in which a line and plummet indicate the angle upon a semicircle graduated in degrees. In general, rainfall lost by run-off increases with the angle of the slope, and the water absorbed correspondingly decreases. In two or more areas essentially similar in soil, cover, and rainfall, differences in water content are directly determined by differences in slope.

The surface of a habitat often shows irregularities which retard the movement of run-off and cause more or less of the rainfall to soak into the soil. The soil itself often shows such irregularities, *e.g.* the rocks of boulder and rock fields, the hummocks of meadows and bogs, the mounds of gophers and prairie-dog towns, the depressions and hummocks where great trees have become uprooted in falling, the raised tufts of prairies and sandhills, the minute gullies and ridges due to erosion, etc. The influence of these, though often not great, is always appreciable and, in many cases, of considerable importance. In dry regions, the increase or decrease in water content is clearly reflected in the development of the vegetation. The effects are usually measurable by means of soil samples, but it is impossible to express the character of the surface in definite terms. It must suffice to describe the surface as even or uneven and to indicate the kind and amount of unevenness.

SOIL AIR

The pore spaces of a soil are filled with air and water. After a heavy rain or irrigation has filled the soil interspaces with water and forced the air out, a fresh supply enters as the gravitational water sinks away. Soil has a very porous structure. In fact, only about one-half of its bulk is solid matter. Many plants thrive best in a soil that contains approxi-

mately 40 to 50 per cent of its maximum water-retaining capacity. The rest of the interspace, about 20 per cent of the volume of a soil in good tilth, is filled with air. Dry soils contain much more air. Frequently, cultivated soils, during periods of drought, are too loose and dry for proper root development, and the plant is thus deprived of nutrients which the soil contains. Conversely, water-logged soils have no air except that dissolved in the water, but certain plants grow well even under this condition. The pore space increases with fineness of texture, degree of granulation, and abundance of organic matter. Thus, the total pore space of a sandy soil may be only 30 per cent of its volume, that of a loamy clay 45 per cent, but a heavy clay may have over 50 per cent. Soil in good tilth is filled with air spaces which are more or less continuous from the surface to the subsoil. Cracks, burrows, and spaces left by decayed roots, as well as the removal of water by absorption promote gaseous exchange among the different soil horizons. There seems to be a steady and fairly rapid exchange between the soil and atmosphere, air entering and passing out both by direct streaming and by diffusion. Variations in water content and temperature, and fluctuations in atmospheric pressure, promote the exchange.

Composition of the Soil Atmosphere.—Because of its proximity to roots and microorganisms, both of which constantly give off carbon dioxide and absorb oxygen, soil air is very different in composition from the ordinary atmosphere. It often contains much more carbon dioxide, 0.2 to 5 per cent or even more, the amount increasing with depth, accumulation of organic matter, abundance of roots, etc. The proportion of oxygen is, moreover, less, and water content much greater and more constant than in the air above ground. The soil air is not static but, like the soil itself, constantly undergoing change.

Soil air is either in direct contact with roots and microorganisms or separated from them by only a thin film of water or colloidal matter. Within these films, the oxygen supply is very limited and the carbon-dioxide content very high, as much as 99 per cent having been found.[422]

Oxygen is important in the process of breaking down insoluble minerals into a soluble form and the consequent enriching of the soil solution. This gas is no less important in the transforming of plant and animal remains into a condition where their nutrient materials become soluble and may be absorbed by plants. Biochemical oxidation proceeds rapidly, when conditions are favorable, and much oxygen is incorporated in the compounds produced.

Relation to Biological Activities and Production of Toxins.—Oxygen is also necessary for the germination of seeds, root growth, root-hair development, and absorption by roots. Without it, nitrification would stop, and earthworms and most other soil organisms would cease their activities. A few microorganisms could get their oxygen supply anaero-

bically by breaking down valuable compounds, such as nitrates, and would thus decrease the soil productivity.

Even roots can carry on respiration for a time without free oxygen, *i.e.* anaerobically. Since the anaerobic respiration of plant roots, bacteria, molds, etc., gives rise to organic acids, alcohol, and other toxic substances, aeration is fundamentally connected with the production of soil toxins.[93]

There is no evidence that plants under the usual conditions of soil aeration secrete toxic substances. These sometimes occur, however, in poorly aerated, sour soils deficient in calcium carbonate and in exhausted cultivated soil.[584] They may consist of soluble aluminum, compounds of iron and manganese, and hydrogen ions as well as various organic substances.[421a] They may arise in the process of the decay of roots or from the decay of other organic matter worked into the soil or as a result of acidity. A large number of organic compounds have been isolated from the soil, and many of them, such as dihydroxystearic acid, are distinctly harmful to plants.[453] Soil toxins are often definitely related to deficient aeration and to anaerobic conditions, since they are readily oxidized and usually soon disappear under proper tillage. "Sour" soils such as "sour" bogs owe their nature to the production of organic acids in the presence of a low supply of oxygen. When it is possible to aerate the soil by stirring, "sourness" is easily remedied, since complete decomposition prevents the accumulation of acids. Thus, toxicity is a direct effect of lack of oxygen and it arises, also, from the accumulation of carbon dioxide in harmful amounts and in connection with the accumulation of organic acids and other compounds. Organic acids seem to result from anaerobic respiration of plant roots and of microorganisms. Inorganic toxins, such as mineral acids, may arise as a result of chemical processes or by adsorption. The absence of any general toxic effect in natural vegetation is demonstrated by the fact that the number of individuals and often the number of species increases as succession progresses toward the subclimax or climax stage.

SOIL TEMPERATURE

The activities of plants are profoundly affected by temperature. Soil temperature is very important, since it affects the biological, the chemical, and the physical processes in soils. It affects the rate of absorption of water and solutes, the germination of seeds, and the rate of growth of roots and all underground (and, hence, aerial) plant parts as well as the activities of microorganisms. It is a great accelerator of all chemical reactions and affects many physical processes taking place in the soil.[40]

The soil receives its heat directly from the sun's rays, probably from warm rains, and from decaying organic matter. In summer, the surface layers are warmer, in winter the deeper ones. The temperatures of all

layers in which roots exist have a primary significance. The daily range in temperature of the surface soil may be very great. Sometimes it reaches maximum temperatures of 120° to 150°F.[68] Such temperatures may cause destructive lesions on the stems of plants, *e.g.* flax, coniferous and other tree seedlings;[296] frequently, the plants droop and die. Surface-soil temperatures above 130°F. often prove fatal to seedlings, and soil temperature is thought to be one of the important factors controlling the distribution of forest types.[23] Lichens on the thin soils of dark-colored rock can endure even higher temperatures.

At a depth of a few inches below the soil surface, temperatures are not so high or fluctuations so pronounced, and, in moist soil, the daily fluctuation is often only a few degrees at a depth of a foot (Fig. 110).

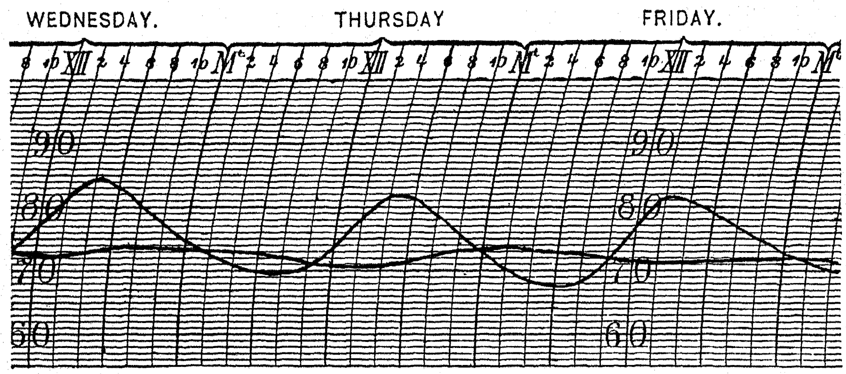

FIG. 110.—Portion of a soil thermograph record from the prairie at Lincoln, Nebraska, during the middle of June; curve with greatest amplitude indicates the temperature at a depth of 3 inches, the other one at 12 inches.

At what time of the day is the soil at 3 inches depth warmest? Coldest? Why is the soil warmest about midnight at 12 inches depth? The air temperature ranged from 45° to 80°F. In a forest the temperature at 3 inches depth is no more variable than that at 12 inches in the prairie. Why?

The annual range in temperature decreases, moreover, with depth. In eastern Kansas, for example, under a grass cover, where the variation of the air temperature was 92°F., it was 48° at a depth of 1 foot, 38° at 3 feet, and 28° at 6 feet in depth. During March there was a complete reversal in soil temperatures, the surface layers which were coldest during winter became warmest and the deeper ones progressively colder. In October the reverse condition occurred.[338] In general, the soil responds slowly to great outside temperatures; roots have a much more uniform environment than shoots. The temperature of soils in the tropics may remain practically constant to great depths.

Factors Affecting Soil Temperature.—Among the factors that directly affect soil temperature are color, texture, structure, water content, amount of humus, and the slope of the soil surface with respect to the sun, as well as the presence or absence of a cover of vegetation. Of all these factors, water content is the most important for the reason that

water has a specific heat about five times greater than that of the solid constituents of the soil.[73] This explains why wet soils are colder in spring than drier ones and why a heavy rain in summer lowers the temperature of the soil. Clay and peat soils are colder than sandy or loam soils, largely because of their greater water content. A dark-colored soil absorbs more heat and so warms up more rapidly than one of lighter color which reflects the rays. This phenomenon is shown by the melting of snow under leaves or bits of wood and their sinking below the general surface. In fact, the melting of snow may be greatly accelerated by sprinkling it with charcoal, a common practice in vineyards and orchards on mountain sides in southern Europe.

Soil Temperature.—The following four experiments should be performed on the same day, employing seven flats and eight accurate thermometers.

Effect of Slope upon Soil Temperature.—Fill three flats at least 3 inches deep with thoroughly mixed, black soil of good water content. Firm the soil compactly into the flats so that each has a level surface. Place the flats out of doors in an unshaded spot the day preceding the experiment so that the soil may take on the outside temperatures. Tilt one flat toward the south at an angle of 20°, and the second toward the north at a similar angle, but place the third in a level position. On the morning of a clear, warm day, place one thermometer bulb in the center of each flat at a depth of ¾ inch. Cover the stem with the case and read every hour during the day. Express the results in the form of graphs. At noon, hold a cardboard 1 decimeter square at right angles to the sun's rays on each of the three flats and measure the length of the shadow cast on the surface of the soil. Multiply each number thus obtained by 10, the width of the shadow in centimeters, and thus determine the number of square centimeters over which a unit area of radiant energy (1 square decimeter) is dispersed.

Effect of Water Content on Soil Temperature.—Use two flats with fairly dry, black soil. Determine the surface area of one flat (*e.g.* 14 by 14 inches) and slowly add enough water (at the temperature of the soil) from a sprinkler to equal ½ inch of rain (14 by 14 by 0.5 = 98 cubic inches, and 1 cubic inch = 16.4 cubic centimeters). Determine the temperature in each flat as before. Express the results in graphs.

Effect of Color on Soil Temperature.—Use a flat filled with light-colored sand. Over a 25-square-inch surface of the flat spread a pint of dry sand previously colored with 4 ounces of black ink. Determine the relative temperatures as above under the two conditions. Plot graphs.

Effect of Cover on Soil Temperature.—Cover one flat, filled with loam as in the previous experiments, with a mulch of ½ inch of dead grass or leaf litter held in place by a fine woven wire of coarse mesh. Compare the hourly temperatures at a depth of ¾ inch with that of the control. Analyze the effect of the various factors in each and compare the four studies upon this basis.

Measurements of soil temperatures should also be made in different habitats and at various depths in the field. A sharp-pointed rod is useful in making a hole for the thermometer.

The degree of slope has a marked effect upon the amount of radiant energy received by the soil (Fig. 111). A slope of only 5 degrees may be equivalent to a latitudinal distance of 300 miles.[9] The soil warms more

quickly, vegetation starts earlier, and crops like wheat may ripen several days earlier on south than on north exposures.[486] Delay in blossoming and consequent reduction of the danger of freezing of fruit trees is often brought about by planting orchards on north slopes. Slope is emphasized by latitude. In the far North, barley, for example, may be grown on south slopes, those facing north being covered until midsummer with snow.

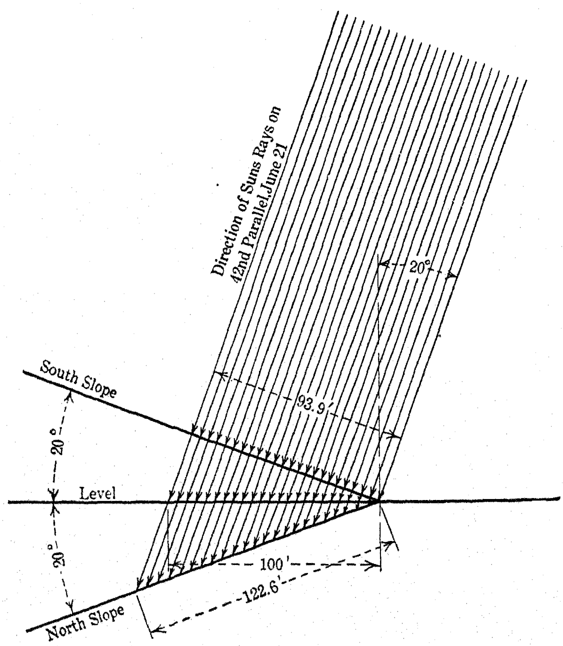

FIG. 111.—Diagram showing the distribution of a given amount of radiant energy on different slopes on June 21, at the 42nd parallel North, *i.e.* in the latitude of Chicago. (*From Lyon and Buckman. The Nature and Properties of Soils. Copyright* 1922 *by The Macmillan Company. Reprinted by permission.*)

Cover has considerable effect on soil temperature. Soil is cooler in summer under a cover of vegetation such as grasses, and especially under forest litter, and warmer in winter than similar bare soil.[312] The effect on depth of freezing is often marked, as it is also under a cover of snow. For example, under clean cultivation the soil at Lincoln, Nebr., froze to a depth of 19 inches, but under a cover crop of millet to only 12 inches. After a snowstorm, accompanied by wind, less than an inch of snow was held on the otherwise bare soil which froze to a depth of 16 inches; 11 inches accumulated in the cover of millet and the soil was frozen to only 8 inches in depth.[155] It is significant that soil does not freeze until it is cooled several degrees below 32°F., and, indeed, some water remains in the liquid form at extremely low temperatures.[41]

Measurement of Soil Temperatures.—The daily range of temperature in the surface of the soil may be considerably greater than that of the air above, and for a study of surface conditions the thermograph is essential. This consists of a metal bulb an inch in diameter and 12 inches long, filled with a liquid which in expanding or contracting records the change upon a metal disk to which it is connected by a long, flexible tube. A pen, connected to the disk, records the temperature upon a sheet which is marked off in degrees, hours, and days and is attached to an 8-day clock which causes the drum to make one complete revolution each week (Fig. 112).

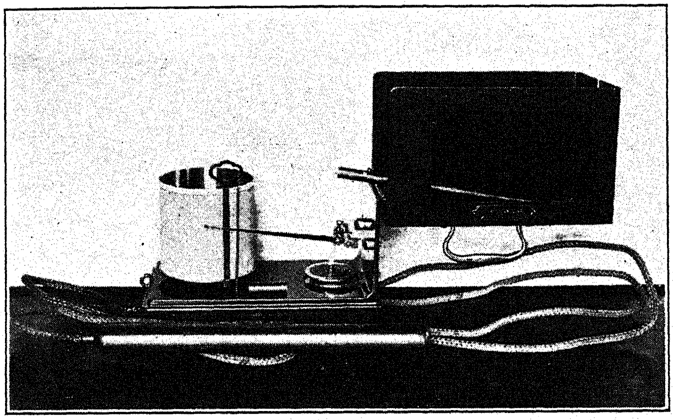

Fig. 112.—Soil thermograph with case opened and a thermometer with brass case placed in the top. The thermograph bulb is buried in the soil at any desired depth.

In setting the instrument in the field, the tube is placed horizontally in a container filled with water. After 10 or 15 minutes, the temperature of the water is carefully determined by means of a thermometer which has been checked by a standardized one and the pen set accordingly, by means of the adjusting device, care being taken to turn the drum so that the correct hour is indicated. In placing the bulb in the soil, great care should be exercised to disturb the natural cover as little as possible, and after adjusting it horizontally at the desired level and burying the surplus tube-length at a similar depth, the natural cover, in so far as possible, should be restored. The exact position of the bulb should be marked. It should be placed at such distance from the instrument shelter that the soil will at no time be shaded by the latter. The shelter should be firmly held in place by means of stakes. Once properly adjusted the instrument needs little attention except to ink the pen, insert a new record, and wind the clock once each week. The readings should be checked from week to week by inserting the thermometer in a small hole made by a sharp rod in the soil near the bulb. The best time is in the early morning when

radiation and absorption of heat from the surface soil are about equal. Otherwise, the reading of the thermograph is apt to lag behind that of the thermometer.

The depth at which the bulb is buried varies with the purpose of the reading. Surface temperatures may be taken by covering the bulb with only a thin layer of soil. If temperatures for seed germination are desired, it should be placed shallower than that for the study of the root development of seedlings. If only one instrument is available a depth of 4 inches is the one usually employed.

Special soil thermometers possess a very long tube, the whole instrument being encased in a wooden jacket for protection. The soil thermometer is placed in the ground at the desired depth. The scale is then above the surface where it may be read directly. Such thermometers, however, are relatively expensive; their placing requires considerable time and trouble; and their use is restricted to the few places where they would be entirely free from disturbance. Since soil temperatures are relatively constant, especially at depths greater than 6 inches, frequent readings of them are consequently unnecessary. Ordinary thermometers, furnished with brass cases to avoid breakage in carriage, yield satisfactory results.

Soil temperatures are usually measured in connection with water-content determinations, the hole from which the soil sample is taken serving for the temperature reading. Immediately upon removing the sample, a thermometer is lowered, with an attached string for great depths, and the bulb left in contact with the soil several minutes, while the duplicate sample is taken, to make sure that the mercury indicates the proper temperature. The thermometer is then raised quickly to the top of the hole so that the upper end of the mercury column can be read. With a little practice, this can be done very easily before the column begins to rise or fall. Care should be taken so that no soil crumbles and falls into the hole. When several soil readings are taken in one day, shallow holes may be made quickly by means of a steel stake, and the bottom of the deeper ones made with the geotome may be used repeatedly without appreciable error if the holes are kept closed by means of cork stoppers. If readings are made on different days, it is desirable to bore new holes.[539]

Relation to Activities of Higher Plants.—The rate of absorption, like all the physical and chemical processes taking place within the roots, is decreased by a lowering of the soil temperature. A low temperature permits only a slow rate of water absorption. Even in the latitude of southern Arizona, the conditions of soil temperature for most favorable water absorption do not prevail in winter, and the effect is a limitation of the development of both root and shoot of winter annuals.[71] This also explains the damage often done to trees, shrubs, winter wheat, and other plants in early spring by warm weather and high winds when the soil is

still cold, if not frozen. Under these conditions, transpiration exceeds absorption. Winterkilling is, perhaps, more often due to drying than to freezing.

Favorable soil temperatures promote rapid seed germination and seedling establishment and are necessary for vigorous root growth. The warmer the soil in spring in temperate climates the more rapid are germination and growth. Plants vary a great deal in regard to temperature requirements for germination. Wheat will germinate at a minimum temperature of 40°, maize requires 49°, but pumpkins require 52°F. Wheat germinates best at 84° but reaches its limit at 108°, but the optimum for maize and pumpkins is 93° and they continue to germinate until 115° is reached.[204] Seeds buried in duff under a dense forest canopy often remain dormant because the temperature is not favorable for germination. Heavy thinning or cutting may admit sufficient heat to promote a good stand of seedlings.

The most important factor in the control of soil temperature is the maintenance of an optimum moisture supply. This can be promoted by drainage or irrigation, by proper methods of tillage to produce a good soil structure, and by maintaining sufficient organic matter in the soil.

Relation to Soil Organisms and Soil Reactions.—Many desirable biological and chemical soil reactions are retarded or stopped by unfavorable soil temperatures. Most soil bacteria do not become active until temperatures of 45° to 50°F. are attained. Temperatures of 65° to 70°F., which afford good root growth, also promote such changes as the decomposition of organic matter with the production of ammonia and the formation of nitrate nitrogen. Likewise, the fixation of atmospheric nitrogen depends upon similar favorable temperatures. In one experiment extending over a period of 3 weeks, the amounts of nitrates produced at 44°, 94°, and 111°F. were 4, 47, and 11 pounds per acre, respectively.[417] Surface-soil temperatures may become so high that bacterial activity is suspended and the organisms themselves may be destroyed.

The rapidity of rock weathering in the tropics illustrates the fact that chemical changes in the soil are greatly accelerated by high temperatures. The solvent action of water is greatly increased. Temperature also exerts a marked effect upon such physical changes as rate of percolation, evaporation, diffusion of gases, vapors, and salts in solution. The aspirating effect brought about by a small change in soil temperature is often so marked as to result in thorough renewal of the oxygen supply of the soil to a depth of several inches.

ALKALI SOILS

In arid regions where drainage is very slight, as well as in marshes, etc., adjacent to seashores and other bodies of salt water, the soil salts may

accumulate to such a degree, especially in lowlands, that they are distinctly harmful to most plants. These accumulations of soluble salts are termed alkali. Alkali in soils includes any soluble salt, regardless of its specific reaction, that occurs in sufficient concentration to injure crop plants. It includes the chlorides, sulphates, carbonates, and nitrates of sodium, potassium, and magnesium and the chloride and nitrate of calcium. Thus, even sodium nitrate, an important constituent of fertilizers, if in excess, produces an alkali soil. All of the alkali salts are

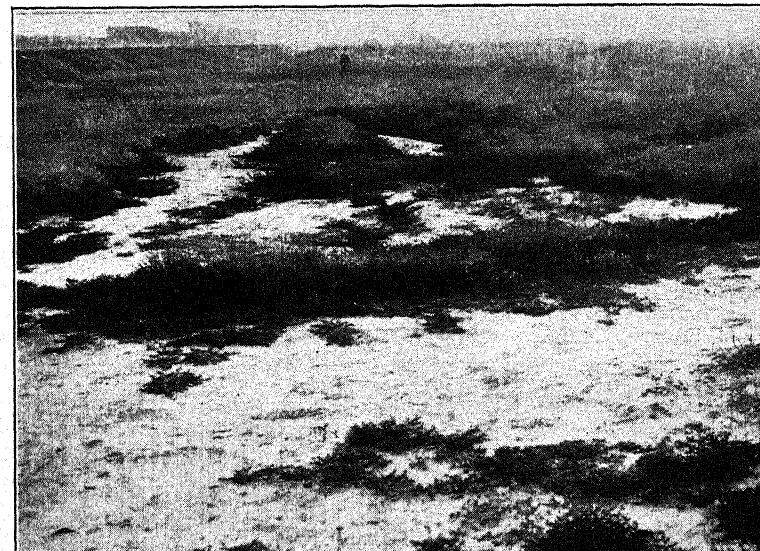

FIG. 113.—An alkaline area due to an excess of sodium chloride. The dark-colored plant bordering the salt-encrusted area is sea blite (*Dondia depressa*), and the lighter-colored vegetation mostly orach (*Atriplex hastata*). Salt grass (*Distichlis spicata*) occurs on the less salty soil in the background.

neutral except the carbonates of sodium and potassium, which are true chemical alkalies. The last two are called black alkali because of the dark-colored incrustation which they produce by their solvent action on the organic matter of the soil. The other alkalies are collectively known as white alkali from the white incrustation usually produced by them (Fig. 113).

White and Black Alkali.—Mix 200 grams of black potting soil with 4 grams of sodium chloride dissolved in 25 cubic centimeters of water and another lot with 4 grams of sodium carbonate. Place each in a glass tumbler and add enough water to saturate. Allow the tumblers to stand where the soil will dry out and note the crust formed in each case. Incrustations of "black alkali" may be white if the soil is very low in organic matter, and the incrustations of "white alkali" may be black if the salts are calcium and magnesium chlorides and the organic matter high.

Alkali areas are very extensive from western Canada to the high plateaus of Mexico and in other arid parts of the world. The salts have originated from the soils derived from the native rock. In regions of greater rainfall, such as the eastern half of the United States, the excess salts have been leached out and finally accumulated in the ocean. Plants of salt water, *e.g.* seaweeds, mangroves, etc., have certain adaptations such as high osmotic pressures or mucilaginous cell contents, etc., characteristic of halophytes.

In about 16 of the western states, soil alkali furnishes one of the chief problems in agriculture. Approximately 13 per cent of the irrigated land of the United States contains enough alkali to be harmful to crops, and over extensive areas the soil is so filled with salts, that only a scanty vegetation can exist.[217]

Why Alkali is Harmful.—Soil alkali is harmful to plants in a number of ways. A concentrated soil solution, due to excess of salts and to loss of water by surface evaporation, may delay seed germination either temporarily or indefinitely by hindering water absorption. The seeds of most halophytes probably germinate only when the soil solution is diluted by rains. If germination is successful, a later concentration of salts may cause the movement of water from the root hairs to the soil. This gives rise to a condition of plasmolysis; absorption is inhibited and wilting and death may result. Even if the plants can grow, their nutrition is deranged, unless they have become adapted to the excess supply of salts. Alkali injury is often shown by chlorosis. The bark of plants may be corroded at the soil surface by alkali salts, especially by the carbonates, concentrating in the surface soils during drought. In this way, the bark on plants in orchards and vineyards may be so thoroughly destroyed that the passage of food from the leaves to the roots is prevented. Alkali carbonates may, moreover, affect soil structure detrimentally, at least to most plants, by dissolving out the humus and deflocculating the clay and by producing, through chemical reaction, impervious colloids. Many alkali soils are underlaid by a hardpan, produced in this manner, which is impervious to both water and roots.

The limit of tolerance to alkali is determined, in part, by the species, a phenomenon clearly revealed in zonation about alkali depressions. Soil samples to a depth of 4 inches from zones of saltwort (*Salicornia herbacea*), sea blite (*Dondia depressa*), and *Atriplex*, at Lincoln, Nebr., where the salt is sodium chloride, reveal a concentration of 2.3, 1.8, and 1 per cent, respectively, of the dry weight of the soil (Fig. 114). Furthermore, tolerance depends upon the kind of alkali. Although sodium carbonate is about as toxic to plants in water or sand cultures as sodium chloride, under natural conditions it is the worst of the alkali salts. This is because of its harmful effect upon the soil also, which intensifies the injury to the plant. The time of concentration of the salt in the

surface soil is also of great importance. Winter wheat, for example, which usually tolerates less than 0.4 per cent, planted in the fall might fail upon an area which would successfully grow spring-sown clover,

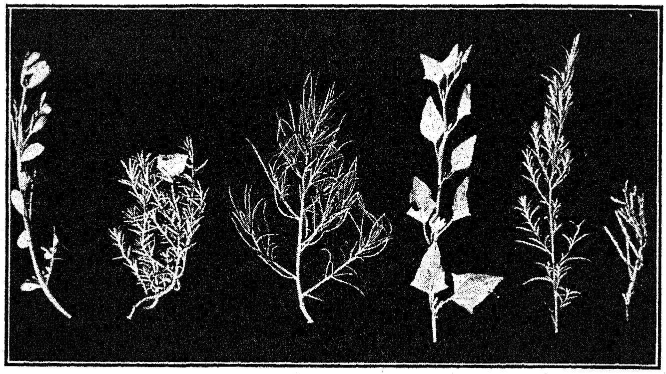

FIG. 114.—Branches from a group of fleshy plants. From left to right, purslane (*Portulaca oleracea*); rose moss (*P. grandiflora*); Russian thistle (*Salsola pestifer*); orach (*Atriplex hastata*); sea blite (*Dondia depressa*), and saltwort (*Salicornia herbacea*).

although the latter is less tolerant of alkali (Fig. 115). Finally, some plants, such as sugar beets and alfalfa, which are very sensitive to alkali injury in their seedling stage, are quite resistant later in life. Because of

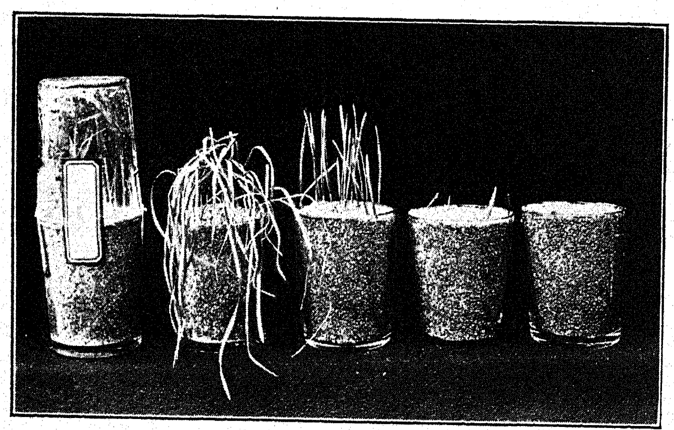

FIG. 115.—Showing method of determining the effects of different concentrations of salt on the germination of wheat. The sand is half saturated with water and contains no Na_2CO_3 (two tumblers on left). The others contain 1,000, 1,500, and 2,000 parts per million of this salt respectively, based on the dry weight of the soil.

complicating factors such as variation in water content (and, hence, dilution of salts), organic matter, antagonism of the salts, adsorption, etc., the degree of tolerance varies within limits.

To Determine the Effect of Different Kinds and Concentrations of Alkali on the Germination of Wheat.—Weigh out 1,000 grams of fairly coarse, dry sand. Place it in a jar and add enough water from a liter graduate to saturate it, noting the amount needed. Measure out enough dry sand to fill three tumblers, and weigh. Also weigh out four more similar lots. To the first lot add 100 cubic centimeters of water containining 1,000 parts per million of sodium chloride based on the dry weight of the soil. Then add enough water to half saturate the sand. After mixing very thoroughly, fill each of the three glass tumblers. Plant 25 selected seeds of wheat about 1 inch deep in each. To prevent evaporation from the surface and consequent increase in salt concentration, invert a second tumbler over the first and keep it in place by means of four large, gummed labels. Label the glasses and place them in rows in the greenhouse in strong, diffuse light.

Proceeding in the same manner, use a concentration of 1,200, 1,500, and 2,000 parts per million, respectively, and also soil without alkali, as a control. In another series, sodium carbonate may be used at the same rates.

At the end of a week, count the seedlings that have appeared above ground in each case and tabulate. Repeat at the end of the second week. At the end of 3 weeks, also count the number of seeds that have germinated but from which seedlings failed to appear. Also, note the nature of the roots and tops of the plants grown under the several conditions. When these results have been obtained, the experiment may be repeated with other concentrations if desired. Explain the effects of an excess of salts upon germination and growth.

In field practice, the degree of salinity is usually determined by the electrical-resistance method. This consists in passing a current through a mixture of 20 grams of soil and 50 grams of distilled water. Resistance varies inversely as the total salt content. This method is not reliable when much organic matter is present. The percentage of the different kinds of salts present can be ascertained only by chemical analyses.[139]

Various methods of reclaiming alkali lands are employed. Among these are scraping the salts from the surface when they have accumulated there; plowing under the surface alkali; leaching the salts into the subsoil and preventing their accumulating at the surface by efficient mulches, etc. The most satisfactory and permanent method is to add sufficient water to leach and drain out the excess salts and thus entirely to free the soil of them.

To Determine Chlorides by Volumetric Precipitation Out of a Chloride Mixture.—Many alkali soils are due almost entirely to sodium chloride. Place 200 grams of oven-dry soil in a liter of water and shake thoroughly from time to time during the following 24 to 48 hours. Allow to settle. Filter twice, taking out all possible cloudiness. Titrate a 50-cubic centimeter aliquot against standard silver-nitrate solution using potassium chromate as the indicator, *i.e.* put a few drops of the indicator (10 grams of K_2CrO_4 dissolved in 100 cubic centimeters of water) into the soil extract and add $AgNO_3$ from the burette. The silver from 1 cubic centimeter of standard $AgNO_3$ solution (4.792 grams $AgNO_3$ per liter of distilled water) unites with 1 milligram of chlorine. Hence, multiply by 20 the number of cubic centimeters of silver nitrate used to neutralize the 50 cubic centimeters of aliquot to find the total amount of chlorine in the 1,000 cubic centimeters of soil extract. Multiply this by the factor 1.6486 to obtain grams of NaCl extracted from the 200 grams of soil. What percentage of salt does the soil contain?

ACID SOILS

In humid regions, the soil is frequently acid. The causes of soil acidity are complex. It is due primarily to the leaching of soluble basic salts, especially calcium carbonate. In soils of organic origin, calcium carbonate originally occurred only in small amounts. When basic salts are present in only very small proportions, the soil develops more or less marked acidity, most generally as the result of the accumulations of humus under conditions of poor aeration, but sometimes by the setting free of acid from the mineral constituents of the soil, as explained below. Either mineral or organic acids may occur. Nitric acid may be produced by nitrifying bacteria; sulphuric acid by the oxidation of sulphur-bearing compounds; hydrochloric acid by the interaction of salt water and soils in the vicinity of saline areas; and carbonic acid is continually produced in large amounts and is universally present in soils. Numerous organic acids, *e.g.* oxalic, lactic, and acetic, are formed by the decomposition of celluloses and other organic compounds, and certain organic acids are actually secreted by roots in poorly aerated soils. Amino acids are also formed by decay of materials of organic origin. It is believed that both the inorganic and organic colloids of the soil adsorb various substances. Probably, by a combination of physical and chemical processes, the molecules, atoms, or ions are adsorbed on the surfaces of the colloidal particles. H ions are among the substances adsorbed. A neutral salt in the soil, *e.g.* calcium chloride, may replace some of the adsorbed H ions, and the latter, going into the soil solution, increase acidity. Moreover, acidity may result from the double decomposition of certain salts already in the soil.[578]

In general, acidity is due to the absence of sufficient calcium and magnesium bases to counteract the acids of whatever origin. The decrease in the amount of bases is brought about by the continual leaching of these soluble compounds. These carbonates, in the presence of acidulated wâter, form the soluble bicarbonates and are carried downward in the soil. When the soil becomes drier, as a result of absorption by roots, they are deposited as the insoluble carbonate, *i.e.* the movement is gradually downward.

Hydrogen-ion Concentration.—The strength of an acid solution is not dependent upon the total quantity of acid present in it but rather upon the number of hydrogen ions in a certain volume of the solution, *i.e.* upon the hydrogen-ion concentration. According to the modern ionic theory, many compounds when in solution undergo electrolytic dissociation into positively and negatively charged particles known as *ions*. In dilute solutions of hydrochloric acid, for example, only a small portion of it is in actual solution as molecules of HCl. The greater portion is almost completely dissociated into positively charged $\overset{+}{H}$ ions and negatively

charged $\overline{Cl}$ ions. The characteristic properties of sourness and reddening of blue litmus are due entirely to the presence in the solution of the H ions. In weak acids, *i.e.* where the acidic properties are only slight, as in vinegar (acetic acid), the molecules are dissociated to only a small extent. There are only a few H ions present in their solutions.

Normal solutions of acetic and hydrochloric acids each contain 1 gram of hydrogen per liter; the total quantity of acidic hydrogen is the same in each. If each solution is greatly but equally diluted (*e.g.* 0.001 N), the hydrochloric acid is 97 per cent ionized, since it is a strong acid; but the weak acetic acid is only 13.6 per cent ionized.[202] The former contains many times more H ions than does the latter. That the *total* acidity of the two acids is the same is shown by the fact that it takes the same amount of an alkali to neutralize each. But since it is the ionized hydrogen only that is responsible for the acidity of a solution at any given moment, it should be clear that the hydrogen-ion concentration of a solution, such, for example, as the soil solution, is, for biochemical purposes, a much more valuable criterion than is the potential alkali-neutralizing power.[350]

Even pure distilled water is ionized to a slight degree. But since there are as many H (acidic) as OH (hydroxyl) ions, the solution is neutral. For convenience, the hydrogen-ion concentration of water is expressed as pH 7.07. Since for pH 7.07 there is exact equality between H and OH ions, it follows that on either side of this value one or the other will be in excess. Thus, values of pH below 7.07 indicate acid solutions—the smaller the value the greater the acidity—and values above 7.07, alkalinity.

Methods of Determining Acidity.—The most accurate method of determining pH is the electrical method depending upon the use of the hydrogen electrode.[84] This method gives a much higher degree of accuracy than is needed in field work, for which colorimetric methods have been devised. These are based upon the fact that a series of indicators have been found whose colors depend upon the prevailing pH and which are sensitive to changes in pH within certain well defined limits. For example, bromthymol blue is yellow for values of pH below 6.5, between 6.5 and 7.5 it changes through various shades of green, until for higher values it becomes blue. Thus, by the use of several indicators, some of which have a lower range of values and others a higher range than bromthymol blue, the degree of acidity or alkalinity of the soil or other solution may be determined.[35,424]

To Determine Soil Acidity.—Use some standard colorimetric method, such as the Wherry double-wedge comparator, LaMotte-Morgan soil-testing set, etc., directions for which accompany the apparatus. Test a number of soils from different habitats and the several layers of the same soil. Do you find a definite relation between acidity and the kind and composition of the plant community?[185,297,425]

Effects upon Plants.—An acid soil solution may affect plant growth by checking the work of nitrifying bacteria and all forms of nitrogen-

fixing bacteria. Earthworms are sensitive to soil acidity. An acid grassplot at the Rothamsted Experiment Station in England contained no earthworms, although they were abundant in an adjoining nearly neutral one.[12,421] The absence of earthworms and general decrease in soil organisms prevent the normal decay of humus and promote the accumulation of carbon dioxide and resulting toxic organic substances. Acidity also has a marked effect upon the availability of soil salts. The solubility of phosphate, calcium, magnesium, iron, aluminum, and manganese is markedly influenced.[224] The harmful effects of acidity may be due to an increased concentration of aluminum or manganese.[288] In acid soil, the crumb or flocculated structure of clay may be destroyed and the soil put in poor physical condition. As a consequence, the water content is increased and aeration diminished. Furthermore, plants need lime, which occurs in too small amounts in acid soils, since it is a necessary nutrient and also acts as a neutralizing and precipitating agent within the cell sap.

Among cultivated plants certain varieties grow fairly well even in soils that are acid.[119,120] Timothy, flax, redtop, and rye belong to this group. These plants have a low lime content, make a relatively slow growth, but possess extensive root systems which thoroughly ramify large volumes of soil. Most leguminous plants grow poorly on acid soils. In general, they are plants of high lime content, make a rapid growth, and, because of their coarse taproot systems, have a relatively medium or low absorbing power for lime. They have difficulty in securing enough lime for their needs.[543] Acidity in soils may be corrected and such soils made more productive to most crops by the addition of some form of lime.

Certain species such as blueberries (*Vaccinium*); mountain laurel (*Kalmia*), and azaleas (*Rhododendron*) grow only in acid soils. This is, perhaps, an adaptation following long periods of adjustment resulting from the sorting out of plants by the process of competition. These acid-requiring plants are, moreover, all endotrophic mycorrhizal species and it seems probable that it is the mycorrhizal fungi rather than the flowering plants themselves that require the acid condition.

Certain species of plants have been grouped into lime-loving (*calciphilous*) and lime-fearing (*calciphobous*) species according to whether they grow on limestone or siliceous soils. Experiments have shown, however, that the calciphobous species, such as the common brake (*Pteris aquilina*), also flourish in a soil rich in lime, provided other soluble salts are not in excess.[575] Similar results have been obtained with the sorrel (*Rumex acetosella*), which has adapted itself to soils so acid as to be unfavorable to most field crops.[580] When lime is added, its yield is increased, but the sorrel is then largely replaced by clover or other plants that can compete successfully in the limed soil.[167,392] Communities developed on soils

with an approximately neutral reaction are usually composed of the largest number of species. The subject is complicated, however, by the fact that the reaction of the soil is often stratified.[423,424] The surface layer may be quite acid, the deeper ones rich in lime, thus presenting two partial habitats. Unless acidity is quite marked, its effects are usually overshadowed by the water and air relations. In bogs, aeration is the dominant factor and acidity is concomitant. A definite correlation between acidity and the presence of sphagnum has been established.[298]

CHAPTER X

RELATION OF UNDERGROUND PLANT PARTS TO ENVIRONMENT

Half of a plant and often much more is frequently hidden from view; rhizomes, corms, etc., are buried in the earth and roots extend far into the soil. Many kinds of bacteria, algæ, and fungi live entirely in this substratum. Because the soil hides the roots from view, they are the least understood, and least appreciated part of the plant. All who deal with plants and vegetation, nevertheless, should have a vivid mental picture of the plant as a whole. It is just as much of a biological unit as an animal, and clear conceptions of the behavior of plants and communities can not be had by a study of the aboveground parts alone. It is important to know not only the usual or normal development and activities of roots but also how these are modified by changes in the soil environment.

Extent of Roots.—Although the roots of some plants are sparse and superficial, in the majority of both native and cultivated species the root systems are, in proportion to tops, deeply penetrating and very extensive (Fig. 116). Those of sweet corn, for example, extend laterally more than half as far as the stalk extends upward, and the root depth is equal to the height of the stalk.[568] The roots of field corn extend 4 feet laterally, and the depth is often 8 feet. The roots of a single plant of cabbage or lima bean thoroughly ramify 200 cubic feet of soil, and those of the tomato are even more extensive. In fact, extensive root systems are the rule among field and garden crops.[565] Many native grasses, legumes, composites, and others have very extensive root systems, penetration to depths of 6 to 15 feet being common.[561] Even the roots of 3-year-old trees and shrubs may spread laterally 3 to 7 feet and penetrate to similar depths.

Rate of Root Growth.—The rapidity of root growth is quite as remarkable as root extent and, like it, is closely correlated with the environment. In many common grasses, the rate of root elongation is over ½ inch per day. Roots of the primary system of winter wheat have been found to grow at a similar average rate over a period of 70 days. When the main vertical roots of corn begin to develop, they sometimes penetrate downward, under exceptionally favorable conditions, at the remarkable rate of 2 to 2.5 inches per day during a period of 3 or 4 weeks.[564] The roots of the squash, which spread laterally in the surface foot of soil, sometimes to distances of 20 feet or more, have a similar rate of growth and rapidly

produce a network of branches. A seedling tree of honey locust, although only 13 weeks old and 9 inches tall, produced a widely spreading root

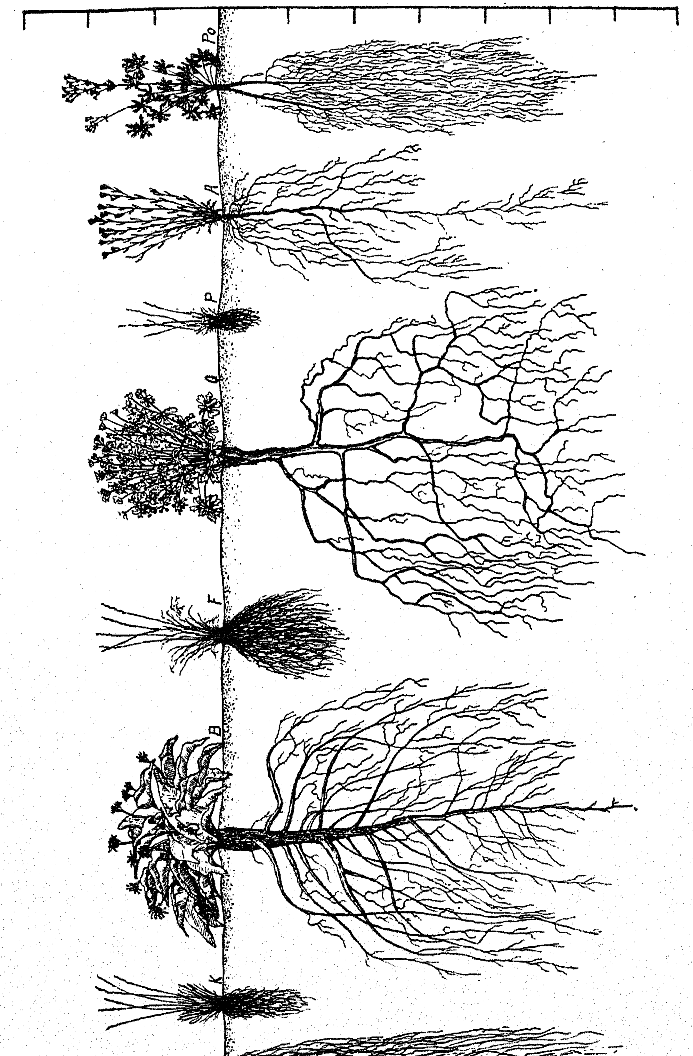

FIG. 116.—Bisect showing root and shoot habit of prairie plants of eastern Washington. *H*, hawkweed (*Hieracium*); *K*, June grass (*Kœleria*); *B*, balsam-root (*Balsamorrhiza*); *F*, blue bunchgrass (*Festuca*); *G*, *Geranium*; *P*, a bluegrass (*Poa sandbergii*); *A*, a composite (*Hoorebekia*); *Po*, cinquefoil (*Potentilla*).

system that extended well into the fourth foot of soil. Other native species often develop with equal rapidity when the soil environment is most favorable for root growth.

Activities of Roots in Subsoil.—The great extent of the root systems of most plants and their usual thorough occupancy of the subsoil have led to investigations concerning their activities at these depths.[126] Experiments have shown that the roots are active in the absorption of both water and nutrients to the maximum depth of penetration. In one experiment, barley was grown in the field in large cylindrical containers 18 inches in diameter and 3.5 feet deep. The containers were filled in such a manner that each 6-inch layer occupied the same depth in the container that it had formerly occupied in the field. Each layer of soil, of known optimum water content, was separated from the one above and below by a thin wax seal. The seals effectually prevented the movement of the water from one soil layer to another but permitted the roots to develop in a normal manner. When the crop was ripe, it was found that the water had been absorbed from the several levels in the following amounts, beginning at the surface: 20, 19, 16, 16, 14, 12, and 11 per cent, respectively, based on the dry weight of the soil. It was, moreover, further ascertained from barley grown in other containers and examined at various intervals, that during the period of heading and ripening of the grain, the bulk of absorption was carried on by the younger portions of the roots in the deeper soil. Similar results were obtained with various other plants.

In other experiments, measured amounts of nitrates (400 parts per million of soil) were placed in the soil at various levels. Corn, for example, removed 203, 140, and 118 parts per million, respectively, from the third, fourth, and fifth foot of soil. Thus, the materials necessary for food manufacture were taken from the deeper soil in considerable quantities, although to a lesser extent than from the soil nearer the surface, which the roots occupy first and where they absorb for the longest time at least in annuals. The deeper portions of the root systems are often particularly active as the crop approaches maturity. Nutrients absorbed by them may produce a pronounced effect both upon the quantity and upon the quality of the yield. Many native species must absorb their nutrients from the subsoil, *i.e.* below a depth of 2 to 3 feet, as is clearly indicated by the root habit. Little or no branching occurs in the surface layers, and structural changes, such as the production of an abundance of cork, preclude absorption by the main root. Thus, the student of environment must consider not only the conditions in the surface soil but also the whole substratum to the depth of root penetration.

Value of a Knowledge of Root Relations.—A knowledge of root development and distribution and of root competition under different natural and cultural conditions is not only of much practical value, but also it readily finds numerous scientific applications. The phenomena of plant succession, whether ecesis, competition, reaction, or stabilization, are controlled so largely by edaphic conditions and particularly by water

content that they can be properly interpreted and their true significance understood only by a thorough knowledge of root relations. It is an aid

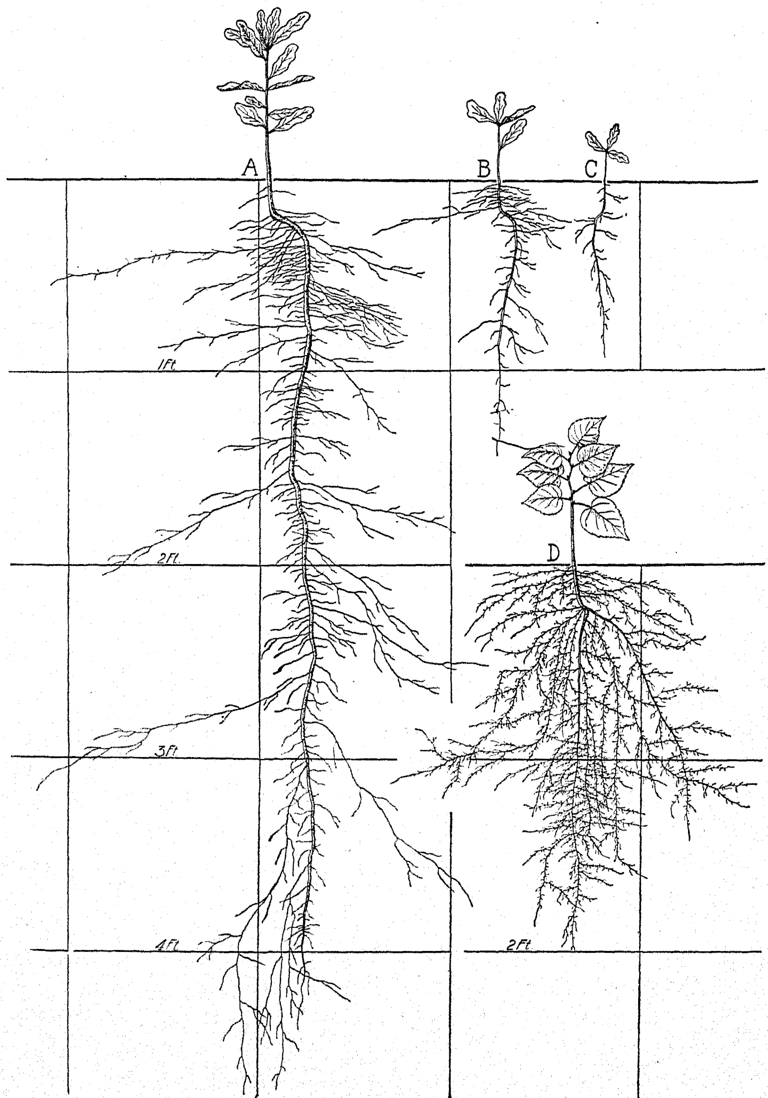

FIG. 117.—One season's growth of bur oak (*Quercus macrocarpa*): *A*, in a clearing; *B*, in a bur-oak forest; and *C*, in a linden forest. The soil in all three habitats was moderately moist but the light in the oak forest was 5 to 20 per cent and in the linden forest only 1 to 8 per cent of that in the clearing. *D*, linden (*Tilia americana*) grown in a clearing, at the end of the first summer. Its roots are not so well adapted to upland soils as are those of the bur oak. (*After A. E. Holch.*)

to the forester in selecting sites for reforestation and afforestation. Yellow pine, for example, because of its prompt germination and immedi-

ate deep rooting, can grow on dry, warm slopes. Likewise, Douglas fir germinates quickly and produces roots 6 to 8 inches deep during the early part of the season. It thus becomes established where the slower growing and more shallow-rooting spruce, hemlock, and cedar fail[243] (Fig. 117).

A knowledge of root relations leads to the intelligent solution of problems of range management and improvement and, indeed, to all problems where natural vegetation is concerned. For example, land is classified upon the basis of the kind and development of the natural vegetation, into that fit for agriculture, that which will grow forests, and that of value for grazing only. Obviously, the root habits are of great importance in indicating the water and other soil relations. When they are taken into account, the natural vegetation may indicate not only the possibilities of crop production but also the kind of crop that can be most profitably grown.[461]

It is an interesting fact that in both field and garden the part of the plant environment beneath the surface of the soil is more under the control of the plant grower than is the part which lies above. He can do relatively little toward changing the composition, temperature, or humidity of the air or the amount of light. But much may be done by proper cultivating, fertilizing, irrigating, draining, etc., to influence the structure, fertility, aeration, and temperature of the soil. Thus, a thorough understanding of the roots of plants and of the ways in which they are affected by the properties of the soil in which they grow is of the utmost practical importance. Something must be known of the character and activities of the roots that absorb water and nutrients for the plant and the position that they occupy in the soil before other than an empirical solution can be had for the following problems: What are the best methods of preparing the land for any crop, the type of cultivation to be employed, the best time or method of applying fertilizers, the application and amount of irrigation water, kind of crop rotations, etc.? A complete scientific understanding of the relation between soil and crop can not be obtained until the mechanism is understood by which the soil and the plant are brought into favorable relationships, *i.e.* the root system.

RESPONSE OF ROOTS TO ENVIRONMENTAL FACTORS

Roots, like aboveground parts, are profoundly affected in activity, external form, and structure by change in environment. The habits of roots, moreover, like those of shoots, are more or less characteristic for every kind of plant.

Heredity.—The primary form of the root is governed, first of all, by the hereditary growth characters of the species or variety (Fig. 118). Some species have taproots that develop rapidly and penetrate deeply,

others branch near the soil surface and the taproot soon loses its dominance, still others are characterized by fibrous roots which may spread widely or penetrate nearly vertically downward. Great variation occurs within a genus and sometimes within the species or variety. One blazing star (*Liatris punctata*) has a strong, much branched taproot reaching depths of 13 feet, another (*L. scariosa*) possesses a large number of fibrous roots originating from the base of a corm. Field corn typically has three roots in its primary root system; in sweet corn there usually is only one. The root system of the garden beet is somewhat different from that of the sugar beet though both belong to the same species (*Beta vulgaris*), and very different from that of the chard (*B. vulgaris cicla*).[568]

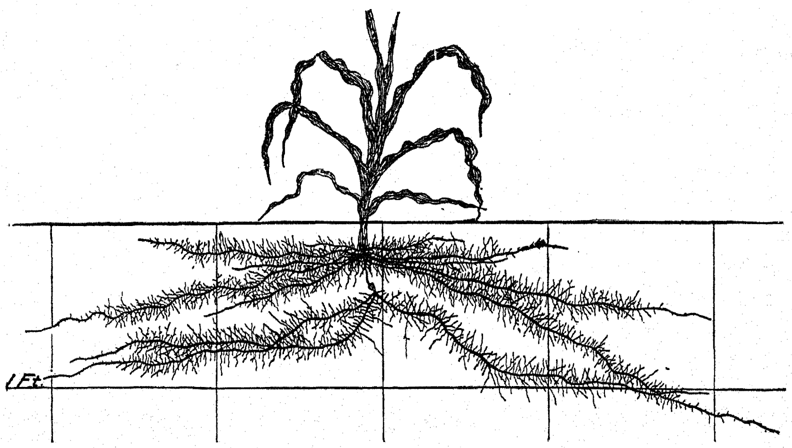

FIG. 118.—Dent corn 36 days old, scale in feet.

Inbred strains of corn differ greatly in the character and extent of their root systems. Certain strains have such a limited and inefficient root system that they are unable to function normally during the hot days of late summer when the water content is low. Selective absorption by individual corn plants is thought to be an important heritable character.[240,246] It has been shown that the form of the fleshy portion of the roots of mangels and sugar beets is a heritable character. Where a dwarf variety of peas having a shallow root system was crossed with a tall variety having a deep one, it was found that the root characters are hereditary and segregate out in the second generation according to the Mendelian ratios.[260]

There is evidence that after long periods of time, during which the soil conditions have had time to impress themselves upon the variety of plants, by a process of natural selection a condition of equilibrium between the type of plant and the soil may be attained. The roots of flax, for example, grown for centuries on the black soils of the peninsula of India, are deep, somewhat sparse, and well adapted to ripen the plant quickly

with the minimum of moisture. Varieties on the well watered but poorly aerated alluvial soil have a well developed but superficial root system. When the flax from the black soils is grown on alluvium, the deep, sparse root system is developed although it is fatal to the well-being of the crop. When the experiment is reversed and the type which suits the alluvium is grown on black soils, there is, again, little or no adaptation to

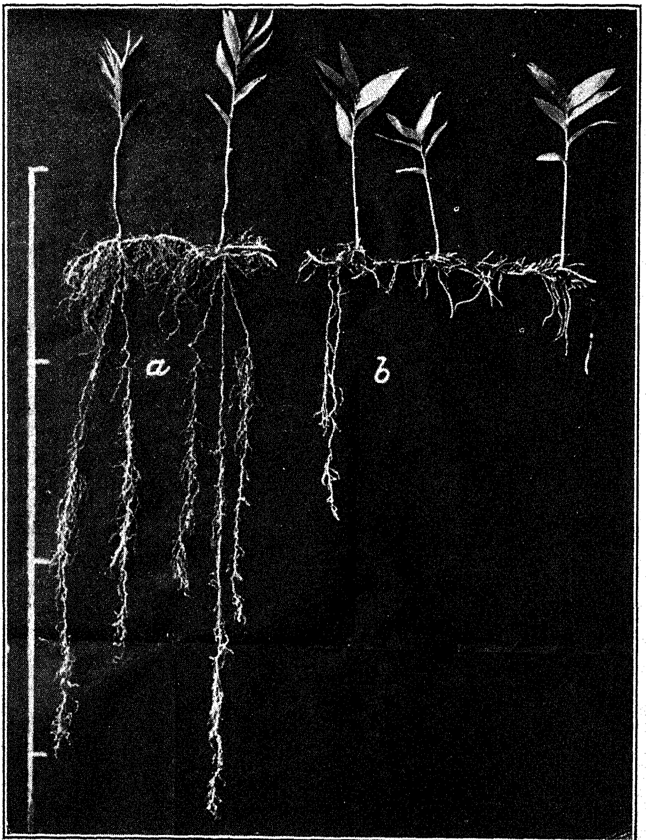

FIG. 119.—Plants of false Solomon's-seal (*Smilacina stellata*): *a*, from a gravel slide; *b*, from a spruce forest. Scale in feet.

fit the new conditions. The root systems of the varieties are just as characteristic and just as fixed as the differences in seed and other above-ground characters of these plants.[250] Heredity in root habits deserves further investigation.

Environment.—Within the species or variety, root modifications are usually brought about by the operation of such factors as water content, aeration, soil structure, and nutrients. In fact, the character of the root system is usually an indicator of soil conditions. By more or less

profound modifications of their root systems, many plants become adapted to different soil environments; others are much less susceptible to change. Among forest trees, for example, the initial or juvenile root system of each species follows a fixed course of development and maintains a characteristic form for a rather definite period of time following germination. The tendency to change when subjected to different external conditions becomes more pronounced as the seedlings become older. But some species exhibit much earlier tendencies to change than others, and widely different degrees of flexibility are also shown. Hence, certain species, such as red maple (*Acer rubrum*), are able to survive, at least for a time, in various situations from swamps to dry uplands. The roots of others, such as bald cypress (*Taxodium distichum*), are so inflexible that they can grow only under certain favorable conditions and their distribution is thus greatly limited.[537] Great variability also occurs in the rooting habits of cultivated trees. For example, the wide adaptation of black walnut to so many soils that it is almost universally used as stock for the English walnut in California is well known. Other fruit trees show much less plasticity, certain varieties failing unless grafted on other stock the roots of which adapt themselves to soils underlaid with alkali or containing excessive moisture or to dry situations.

Of 28 native grasses and other herbs studied in two or more widely separated habitats, 25 showed very striking changes in their root habits as to depth of penetration and position and number of branches; one exhibited only moderate differences, and two showed practically no change (Fig. 119). The roots of many cultivated crops of field and garden are very plastic, responding readily to environmental change. Sometimes the root variation is so great and the growth habit so profoundly changed that the roots are scarcely recognizable as belonging to the same species.

Response to Low Water Content.—A relatively low water content, provided there is enough to insure good growth, stimulates the roots to greater development, resulting in a greatly increased absorbing surface. Corn grown for 5 weeks in a moist, rich, loess soil (available water content 19 per cent) had a total root area which was 1.2 times greater than that of the transpiring surface of stems and leaves. Corn, with similar hereditary characters, grown in like soil, with an available water content of only 9 per cent, had a root area 2.1 times greater than that of the tops. The total length of the main roots in the two cases was about the same, as was also their diameter. In neither case did the main roots make up more than 11 per cent of the total absorbing area. In the drier soil, 75 per cent of the area was furnished by the primary laterals and the remaining 14 per cent by branches from these, but in the moister soil the primary branches furnished only 38 per cent of the root area. It seems as though the plant had blocked out a root system quite inadequate to meet the

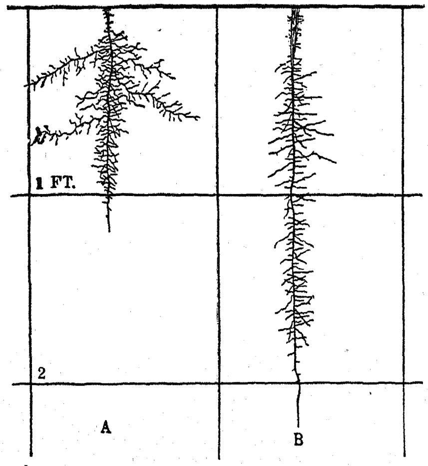

FIG. 120.—Sugar beets about 2 months old: *A*, dry land with practically no water available in the second foot; *B*, irrigated soil.

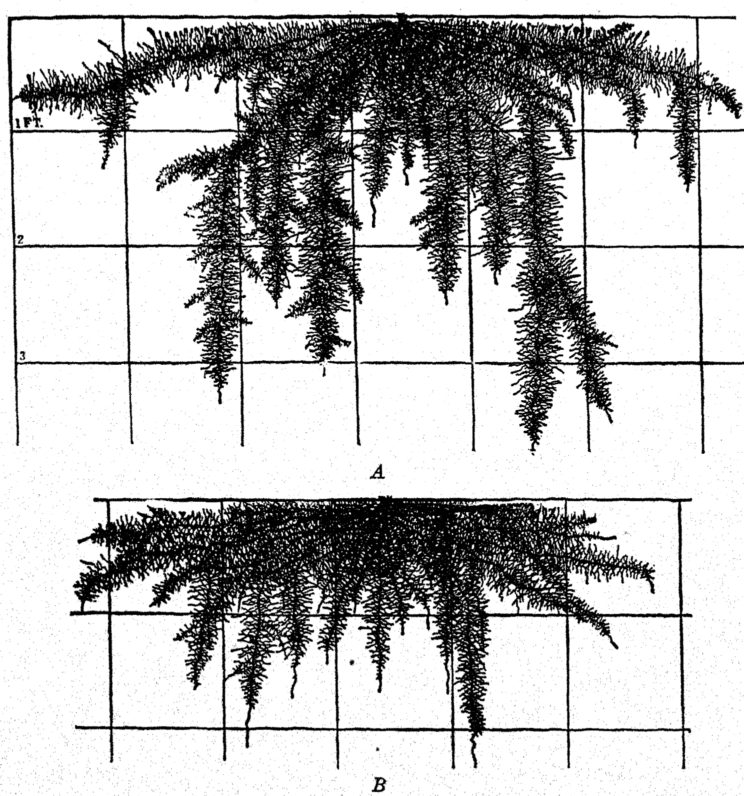

FIG. 121.—Roots of dent corn 8 weeks old: *A*, grown without irrigation, only 2 to 4 per cent of water available at any depth; *B*, fully irrigated in fertilized soil. The heights of the stalks were 2 and 3 feet, respectively.

heavy demands for absorption made by the vigorous tops, and as the soil became drier the remaining 51 per cent of the area was furnished by an excellent development of secondary and tertiary branches.

Maize in loess soil with only 2 to 3 per cent of water in excess of the hygroscopic coefficient had about one-third more laterals than in a similar soil of medium water content, in proportion to the length of the main roots. The absorbing area, moreover, in comparison to tops was greater. Similar results were obtained with 2-months-old alfalfa,

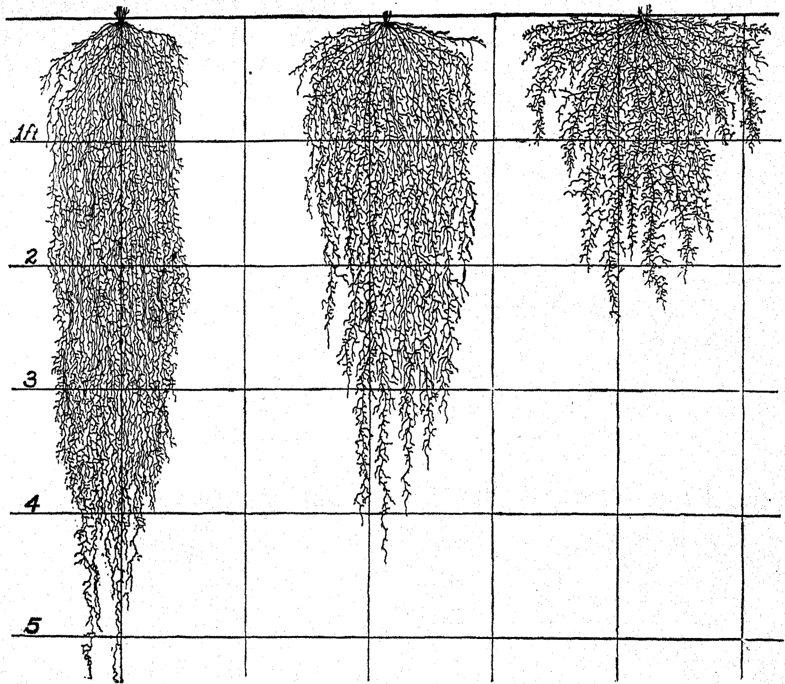

FIG. 122.—Average root development of winter wheat in fertile silt loam soils under a precipitation of 26 to 32 inches (left), 21 to 24 inches (center), and 16 to 19 inches (right). Average from studies made in 20 fields.

although here the area of the taproot system was exceeded by that of the tops. Thus, a low water content, within certain limits, stimulates increased root development.

Figure 120 shows the difference in the root habit of seedling sugar beets due to water content, and Fig. 121 the effect upon root development of corn. In the latter case, the corn grown in irrigated soil had about 12 branches per inch of main root as compared with 27 in dry land. Branches in the drier soil were, moreover, twice as long and had approximately twice as many sublaterals. Such a root system, of course, is much better fitted to withstand drought, and its wide distribution throughout the soil mass brings it in contact with a greater supply of

nutrients. It should be clear, however, that the ideal root system is not necessarily one with the most extensive branching but one that fully occupies the soil to an adequate depth and throughout a radius sufficient to secure at all times enough water and nutrients. Where the soil is very dry, root development is greatly retarded or even ceases, and the aboveground parts are consequently dwarfed. For example, on the short-grass plains, roots of alfalfa and wheat, which normally penetrate several feet deep, although more profusely branched, are almost entirely confined to the surface 2 feet of soil because of lack of sufficient water in the subsoil to promote growth (Fig. 122).

To Determine the Effect of an Excess or Deficiency of Water on Plant Growth.—Fill three large pails, at least one of which is of galvanized iron and will hold water, with air-dry potting soil to within 2.5 inches of the top. Add 2 inches of soil of good water content. Plant seeds of sunflower and cover the soil with a mulch of coarse sand or fine gravel ½ inch deep. Water sparingly if needed. When the cotyledons are unfolded, thin the plants to about five well-spaced individuals per container. To the metal container (hydric series) add enough water each day so that water stands on the surface; to the mesic one give enough to moisten thoroughly the soil throughout; but to the xeric one add only enough water (daily, if need be) to keep the plants from badly wilting.

When the mesic plants have reached a height of 8 to 12 inches and have produced several pairs of leaves, cut the plants in all the containers at the ground line. Wrap each lot separately in moist paper to preserve for further study. By means of a trowel and ice pick make an examination of the root extent under each condition of growth. Secure a root system as complete as possible from each container. Wash away the soil and float the roots out in shallow black trays. From this study and that of the tops, complete the following table:

Character	Xeric	Mesic	Hydric
Depth of penetration, centimeters			
Approximate lateral spread, centimeters			
Number of secondary laterals per centimeter			
Number of tertiary laterals per centimeter			
Relative abundance of root hairs			
Average height, centimeters			
Average diameter of stem, millimeters			
Average number of leaves			
Average leaf area, square centimeters			
Average dry weight, grams			
Other characters, *e.g.* color, pubescence, evidence of disease, etc			

Response to High Water Content.—Where the surface soil is wet and the water table is at no great depth, plants root shallowly. This is a response to lack of aeration. An extreme case is found in bogs. Here the roots and rhizomes form a mat only a few inches thick above the water level. The roots are superficially placed because the parts assume

the horizontal position above the water level, or the taproot dies and is replaced by horizontal laterals, or, where the roots are all vertical, they die at the water surface.[154] A number of species have only shallow roots where the water table is high but deeper ones in moist peat or mineral soils. Trees growing in bogs are likewise shallow rooted. The larch or tamarack (*Larix laricina*) has no taproot. All the roots are horizontal and above the water level. They are so shallow rooted that trees are sometimes overturned by the wind and the entire root system exposed.

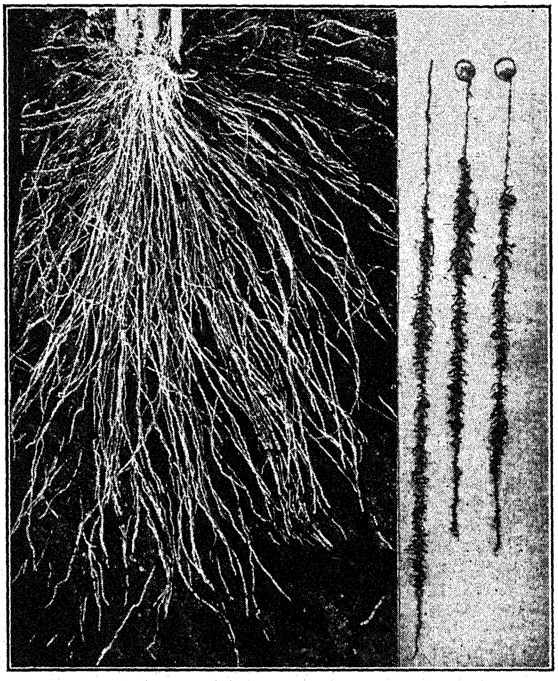

FIG. 123.—Roots of the great bulrush (*Scirpus validus*) about 2 feet long, grown in a saturated soil (left), and a few roots from very dry soil. Note the almost complete absence of branching in the first lot and the marked development of laterals in the second one.

Cedars, spruce, ash, pin oak, etc., when growing in wet soil with a high water table have shallow but widely spreading roots. The same is true of cottonwoods and willows of sand bars and low beaches.

Certain species characteristic of swamps and bogs have roots or rhizomes that grow under water (Fig. 123). Among these are the cattail (*Typha*), great bulrush (*Scirpus validus*), reed (*Phragmites*), arrowhead (*Sagittaria*), cotton grass (*Eriophorum*), birch (*Betula pumila*), water willow (*Decodon*), etc. In certain palms, mangroves, etc., some of the roots grow directly upward. Erect projections from horizontal roots of the bald cypress (*Taxodium*), known as *knees*, develop where the tree grows in swamps.[590] These supposedly are organs for aeration. In

most cases, an oxygen supply is afforded the underground parts of swamp plants by gas exchange through large internal air spaces;[449] in some, *e.g. Salix nigra*, it has been shown that the roots will grow for a time even in the absence of atmospheric oxygen.

Root Habits Modified by Irrigation and Drainage.—Keeping the surface soil too moist during the early life of the plant may promote a more shallow rooting habit, and the crop may later suffer from drought, unless watered very frequently. One of the most difficult problems of irrigation is to apply the water in such a way that plants are not made surface feeders. Otherwise, the natural advantages of the roots widely penetrating the subsoil for nutrients are lost. Conversely, delay in time or amount of water used may tend to promote a deeper rooting habit. The proportion of roots to tops may be definitely increased by decreasing the soil moisture.

Roots respond both in amount and direction of growth to differences in water content and aeration. By varying these factors through the application of more or less water, not only the root system but also the aboveground plant parts and yield may be varied, since a close correlation exists between the growth of roots and tops.

Raising the water table even temporarily by irrigation causes the death of the deeper roots in many plants and usually results in a decreased yield. The roots of some species succumb more readily than others. Among many plants, top development depends upon a sufficient root supply, as was clearly illustrated in the case of the cotton plant. The amount of shedding of leaves and bolls was directly proportional to the extent of the root system that was submerged and died as a result of a rising water table. But when the water table was again lowered, a new growth of tops took place simultaneously with a new growth of roots into the area thus provided for root extension.[18]

The general shape of the root system of trees and other plants may be controlled more or less by regulating, under irrigation, the depth of the water table. If the subsoil is water-logged and thus unaerated, deeper roots will not develop or, if already grown, will soon die as the water table rises. In either case, there is a marked tendency toward the production of an abundance of roots so superficially placed that cultivation results in more or less serious root pruning. Under such conditions, moreover, plants are more sensitive to drought, temperature changes, etc. They require heavier irrigation and greater amounts of fertilizers than those more deeply rooted.

The proper drainage of swamps and bog lands for cultivated crops should be determined with reference to root relations. Extensive experiments have shown that the water table, if at a shallow depth, determines the limit of root penetration and thus, to a large extent, controls the yield of many common meadow grasses, such as timothy,

meadow fescue, and bluegrass.[374] Even when the water table is high, only rarely does a root penetrate into the saturated soil, although in well-drained soils these grasses are quite deeply rooted. In pasture mixtures, this water relation may be an important factor in determining which species will thrive and become dominant and which will disappear. Many coarse marsh grasses and grass-like plants can thrive in wet situations, since the anatomical structure of their roots permits of rapid gaseous exchange. But most cultivated plants require well-aerated soil. For example, corn in well-drained soil frequently penetrates 6 feet or more, but in peat marshes where a system of underdrainage kept the water table almost stationary at about 2.5 feet, the roots, upon reaching a level 18 inches above the water table, where the peat soil was very wet and poorly aerated, turned aside and failed to penetrate more deeply. This inhibition to deep root penetration is clearly reflected in the dwarfed stature and reduced yields of the aboveground parts[153] (Fig. 23).

The maximum depth to which the water table should be lowered depends largely upon the nature of the soil as well as upon the root habits of the crops to be grown. If the soil is coarse and capillary action consequently low, too great lowering of the water table may result in a soil too dry to afford maximum yields. Sugar beets, alfalfa, and other plants with taproots 5 to 20 feet deep require a deeper and better-drained soil than melons or other cucurbits where the main portion of the roots ramifies the surface foot on all sides of the plant to a distance of 15 to 20 feet. For the latter, sandy loams with a clay subsoil are ideal, since they warm quickly and promote rapid root growth but still retain moisture sufficiently well for the shallow root system.

Response to Nutrients.—The response of native plants to nutrients except where they occur in excess (*i.e.* alkali) has received little study, but that of cultivated plants is fairly well known.[555] Crops grown in rich soil have roots that are shorter, more branched, and more compact than those grown in similar but poorer soil. Sachs, over half a century ago, demonstrated that the more concentrated the nutrient solution the shorter the roots, and Liebig stated that plants search for food as if they had eyes. Plants grown in soils with alternate layers enriched with nutrient solution branch much more profusely in these layers. Plants so arranged that one-half of the root system grew in soil rich in nitrates and the other half in poor soil gave similar results. Of course, enriched soil promotes better shoot development, which, in turn, furnishes a greater food supply for further root growth.

To Determine the Effects of Nitrates on Root Development.—Roll pieces of light galvanized iron 12 by 18 inches into the shape of cylinders 1 foot high. Let the edges overlap so that each fits snugly into a ½-gallon, glazed jar. Thoroughly mix a quantity of dry potting soil with half its volume of dry sand. To one lot add 400 parts per million by weight of sodium nitrate dissolved in water. Bring both lots of

soil to an optimum water content. Fill one cylinder with one kind of soil and the second with the other, slightly compacted by jolting, and close all crevices or seams with plasticene or modeling clay. Plant a dozen soaked seeds of barley 1 inch deep in each and then cover ½ inch deep with dry sand. When the third leaf has fully developed, unroll the cylinders and compare the root systems in regard to length and branching. This is best done by floating them in water in black trays.

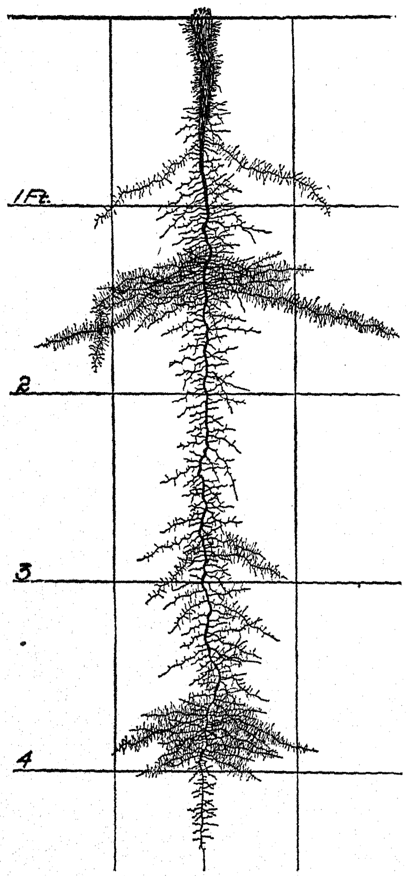

FIG. 124.—Root of sugar beet grown in fine sandy loam soil, showing root stratification in the second foot and fourth foot where layers of clay were encountered.

When roots enter a soil area enriched by the decay of former roots, the greater degree of branching is often very marked. They frequently follow the path of their predecessors for considerable distances, branching in great profusion. Similar branching, which may be due partly to better aeration, frequently occurs in earthworm burrows. Marked contrasts in the degree of ramification of roots as they penetrate different soil strata are often to be attributed to differences in richness of soil. Frequently, root stratification is due to water content, but the factors of water and nutrients often operate together (Fig. 124).

It has been shown experimentally that in every case where roots came in contact with a soil layer rich in nitrates, they not only developed much more abundantly and branched more profusely but also failed to penetrate as far into the deeper soil. On the other hand, it has been shown that wheat and barley seedlings grown in both soil and culture solutions low in nitrates produce remarkably extensive root systems, although the shoots are small. Fertilizing the surface layers of soil with nitrates and thus stimulating surface root production in regions where these layers have very little or no available water during periods of drought appears to be distinctly detrimental to normal crop production. Nitrogen leaches readily and that produced by bacterial action in summer fallow (*i.e.* where the land is cultivated without a crop) may mostly occur at depths of 3 or more feet by the next spring.[493]

The effect of phosphates in promoting root growth in length and number of branches has long been recognized. They are beneficial

wherever drought is likely to set in, because they induce the young roots to penetrate rapidly into the moister layers of the soil below the surface. Wheat, on land treated with phosphates, was found at the end of 3.5 months to be rooted almost twice as deeply as in similar soil to which no phosphates had been applied.[306,557] Nutrients may also affect the size and shape of the fleshy portion of root systems. Potash fertilizers, for example, may result in sweet potatoes being considerably shorter and thicker, while nitrogen in excessive quantities tends to produce long potatoes.[450]

Relation to Alkali and Acidity.—Studies of root systems in soils impregnated with alkali point out clearly that the adaptation of plant to habitat is often largely one of root distribution above or below the layers of greatest salt concentration. Shallow-rooted native species which can not endure alkali may grow upon land which contains alkali at depths below those of root penetration. Orchards and vineyards are sometimes planted in soils of rather high salt content, and the root systems may become thoroughly established in a non-toxic lower layer of soil which is less alkaline than the surface layers.

Deeply rooted plants, such as alfalfa and trees, may penetrate the alkali stratum after getting a start in the surface soil when, because of rain or irrigation, the salts have been leached deeply. Later, as the alkali, because of evaporation of water, becomes more concentrated in the surface, the roots penetrate deeply. In this way, some plants not exceptionally tolerant may withstand what seem to be excessive quantities when the whole absorbing zone is not considered.[217] Alfalfa, sugar beets, and cotton, all of which have seedlings sensitive to alkali, may get a good start due to heavy rains or irrigation which dilute the harmful salts so much that the seedling stage may be safely passed. But if they encounter a strong alkali stratum a foot or two below the surface, these plants may prove less resistant than the fibrous-rooted cereals which may absorb in the upper less alkaline soil. In California it has been found that the roots of lemon are unusually susceptible to alkali injury, while experiments in Australia indicate that the sour orange is the best stock for orange and lemon in sections where the irrigation water may contain considerable alkali.

Extensive investigations on the effect of soil acidity on root development have been made on moor soils in Europe. The roots of cultivated plants were found to penetrate into the soil only as deeply as the addition of basic materials had sufficiently freed the soil of free acids. Certain native species were found to be less sensitive, their roots occurring in the deeper soil. Experiments with potted soils showed that the length of the root system agreed very closely with the depth of the acid-freed root bed. Studies of root development in the field, where the deeper soil layers were freed from acid by the addition of lime, confirmed the pot experiments.

Wheat seedlings grown in nutrient solutions with a high H-ion concentration developed root systems that were abnormal in being short, stubby, and much branched. The protoplasm of the root hairs was found to be coagulated and flocculated, and the hairs were probably rendered ineffective as absorbing organs. Excessive acidity affects the roots of plants by partially or wholly retarding growth in length. The branches are short and end abruptly. The roots often thicken and soon become dull white or yellowish brown in color.[4] Sometimes, as in the case of root rot of conifers, injury to the roots resulting from acidity of the soil leads to infection by fungi which cause root decay.[11]

Response to Soil Structure.—Where other factors are the same, roots penetrate more deeply and spread more widely in soils of loose than in those of compact structure. Layers of compact soil often play an important part in shaping the root system. Western yellow pine seedlings transplanted in clay-loam soils with their roots against one side of a hole show a marked tendency to grow a one-sided root system, the growth being away from the side of the hole and into the looser soil within. When transplanted by the usual "trencher" method, the roots invariably develop only in the plane corresponding to the longitudinal axis of the trench.[544] In plowing for cultivated crops on heavy soils, the depth should be varied from year to year so that a too firm "plow sole" will not develop at a certain level and tend to confine root development to the plowed layer.[264]

To Determine the Effect of Soil Structure upon Root Habits.—Screen about 250 pounds of a fertile, loam soil and bring it to a good, uniform water content. Secure two strong boxes made of durable wood an inch in thickness and well painted, the inner surfaces with asphalt paint. The boxes should be about 10 by 10 inches in inside dimensions and 24 inches deep, one side being held in place by heavy screws. Weigh one box, and then fill it with soil, compacting the soil only by jolting the box repeatedly on the floor during filling. Weigh out 30 per cent more soil than that contained in the first box and fill the second one by tamping firmly with a large wooden tamper each shovel of soil placed in the second box, using the entire amount. Plant seeds of sunflower, wheat, or other plants in a little non-compacted surface soil in each container. It is best to use a single species in each box and to thin the plants to about eight well-spaced individuals. Cover each container with a thin mulch of fine gravel. Water sparingly. When the plants are 3 to 4 weeks old, tilt the boxes at an angle of 45°, take off the sides, and remove the soil about the roots with an ice pick. Determine the depth of penetration, approximate number and spread of lateral roots, whether the taproot is straight or crooked, and any other points of interest. Make a drawing to scale of a typical root system from each environment, and suggest the reasons for the differences obtained.

In heavy clay soil, the fleshy roots of beets, carrots, parsnips, etc., are often irregular and misshapen, as are also those of the sweet potato. Difficulty of root penetration of both main roots and branches is indicated by a tortuous course. The fleshy, cylindrical roots of native plants are sometimes flattened into bands in penetrating rock crevices.

Response to Aeration.—The dependence of root development of most plants upon aeration is clearly shown by water-logging the soil.[31,409] In a few days, the usual cultivated plants turn yellow, show wilting, and may ultimately die. But they may survive submergence for weeks, provided the water is kept well aerated. Even cranberries and blueberries, which will stand submergence for months when inactive, are harmed by water-logging the soil only 3 or 4 days in summer.[32] Rice, too, at least in pot cultures, grows better when the soil is frequently irrigated and drained. The regular presence of air passages or aerenchyma in amphibious and floating hydrophytes, as well as the often constantly open stomata, indicate the importance of a supply of oxygen.

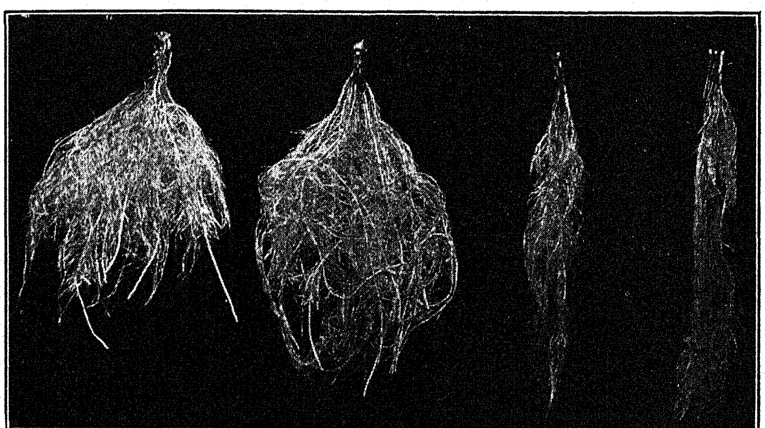

FIG. 125.—Roots of corn grown in water cultures, all about 6 weeks old. Those on the left were constantly aerated, those on the right not at all. The non-aerated plants had only 58 per cent as great a leaf surface and 55 per cent as great a dry weight as the aërated ones.

In nutrient solutions, plants grow best where constant and thorough aeration is given. The superiority of roots grown in aerated cultures is shown not only by their greater weight but also by their greater extent and degree of branching (Fig. 125).

Exclusion of oxygen from the roots of most plants interferes with the respiration of the protoplasm of the root cells, resulting in its death and the consequent failure of the roots to function as absorbers for the plant. The cessation of water intake is soon followed by the progressively decreasing turgor of the shoot and leaves and, finally, by wilting and death.[316] Roots respond somewhat differently to variations in the composition of the soil atmosphere.[286] Roots of the mesquite (*Prosopis*) continue growth for a considerable period of time in a soil atmosphere containing less than 3 per cent oxygen, while those of a cactus (*Opuntia*) promptly cease growing. An increased air supply to the roots of certain species favors root branching and accelerates root growth[254] (Fig. 126).

Plants growing naturally in well-drained soils are much more sensitive to the composition of the soil atmosphere than are those in poorly drained and poorly aerated habitats.[78] Certain deeply rooted species like alfalfa are able to grow for a time in an atmosphere containing only 2 per cent oxygen. It seems probable that one of the beneficial effects of good rains, especially in heavy soils, is the increased oxygen. Although displacing the soil gases, rain water is a solution highly charged with oxygen and has a markedly stimulating effect upon growth.

Orchard trees have been known to die from "puddling" of the soil and the resulting deficient aeration. Also, trees are sometimes killed by cattle trampling and packing the ground about them to such a degree that the air supply in the soil is deficient. In heavy soils, such large

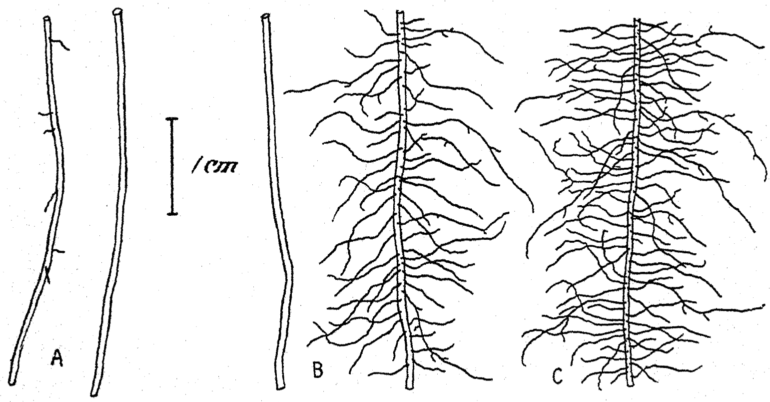

FIG. 126.—Relative branching of roots of cattail: *A*, in saturated soil; *B*, in wet but drained soil; and *C*, in relatively dry soil.

quantities of carbon dioxide may be produced by a sod of grass roots growing under fruit trees that the trees and fruits do not develop normally.[251] It has been experimentally demonstrated that many plants respond to an increased carbon-dioxide content of soil by developing roots which are much shallower and more widely spreading in the surface soil. Carbon-dioxide content of garden soils may sometimes be so high as to be detrimental to the root development of some common species.[371]

A deep, well-prepared seed bed is essential for good aeration, especially in humid regions. It not only promotes plant growth directly by lightening and warming the soil and conserving moisture but also indirectly by promoting various biological activities, especially ammonification and nitrification. The preparation of a good seed bed as against none resulted in an increase in the yield of corn of 14.5 bushels per acre in Illinois.[360] Underdrainage has a very beneficial effect, since large quantities of air move into the interspaces formerly occupied by water.

To Study the Effects of Aeration on the Growth of Roots and Root Hairs.—Secure rhizomes of *Typha* in early spring before growth has begun or in the fall after the soil has been thoroughly frozen. Select eight rhizomes 3 or 4 inches long with good growing points and remove all of the roots. Secure two containers 2 feet deep and 8 to 12 inches in diameter. Place a thin layer of gravel in the bottom of each, after having perforated the bottom of one to afford good drainage. Fill both with screened potting soil. Plant the rhizomes about 3 inches deep, four in each container. Fill one container with water and by stirring somewhat, so that the air may escape, thoroughly saturate the soil and throughout the experiment maintain the water at a level 2 inches above the soil surface. Keep the second lot of soil wet at all times by flooding the surface on alternate days. Catch the water as it drains through in order to use it again.

At the end of 3 or 4 weeks remove the sides of the containers, wash out the root systems, and compare them in regard to differentiation into water and soil roots, length, degree of branching, development of root hairs, etc. A third container with 18 inches of dry soil overlaid with a 6-inch layer of moist soil gives excellent comparative results. Explain the results secured. Which is controlling, water or air?

Response to Temperature.—If other conditions are favorable, roots of various plants will grow at soil temperatures below 40° and as high as 120°F. Little is known of the most favorable temperature for root growth, but for many temperate crop plants it probably lies between 65° and 75°F. It seems probable that species with extensive roots in the surface layers of soil, *e.g.* cucurbits, cacti, etc., grow better at higher temperatures than those with deep roots. Certain cacti make their best root growth at a temperature of 93°F., although the rate of growth is also correlated with the length the root has already attained. It has been found in the case of peas in water cultures that, if insolation is not excessive, the amount of daily fluctuation of root temperature between 44° and 84°F. affected growth but little.

Root growth occurs in certain native species at temperatures so low as to be distinctly unfavorable for others, as has been fully demonstrated. The shallow-root habit of certain desert plants is thought to result from subsoil temperatures too low to promote root growth. The general distribution of many cacti seems closely related to the response of the roots to the temperature of the soil, although the effect of aeration is also a contributing factor.[73,74]

Root systems superficially placed are subject to temperature changes quite unlike those experienced by more deeply seated ones. That soil temperatures have an influence on general plant growth is shown by the practice of florists of using bottom heat for certain plants. Cuttings often require definite soil temperatures for rooting. In some cases, considerable vegetative growth can be produced, despite unfavorable atmospheric conditions, by maintaining a soil temperature favorable for root development.

In regions where plants grow in soil underlaid with a frozen substratum, the decrease in temperature with depth must exert a profound

effect upon root activities. Alternate freezing and thawing of a soil tears the roots and sometimes causes losses of 25 to 50 per cent among forest seedlings.[203] Shallow-rooted plants may be heaved entirely out of the ground. Experiments have shown that there is a direct relation between resistance to winterkilling and the extensibility of roots of certain plants. The roots of certain perennial vegetable crops such as onions and beets were killed at winter soil temperatures of 34°F. and a new root system grown the following spring. Those of carrots partly died, but the root system of parsnips was unharmed.[568]

Aeration and Soil Temperature.—Some fundamental relations exist among rate of root growth, aeration, and soil temperature.[76] Under normal conditions of aeration, the rate of root growth is known to be influenced by soil temperatures in such a manner that there are three well-defined temperatures for growth. These are the maximum or highest temperature at which root growth is possible; the optimum, at which temperature growth is most rapid; and the minimum, below which it ceases. But under a diminished oxygen supply, these cardinal temperatures seem to be greatly modified. As the oxygen supply in the soil air is decreased, rate of growth diminishes in a soil with a high temperature. For example, corn roots, in a soil atmosphere of 96.4 per cent nitrogen and only 3.6 per cent oxygen, at a temperature of 30°C., grow about one-third as rapidly as at the same temperature under normal conditions of aeration. But at 18°C., growth is increased to about two-thirds the normal rate at that temperature (*i.e.* 18°C.) when the soil is well aerated. Similar results have been secured for cotton and other plants, which to attain a fair rate of growth at high soil temperatures must be in a well-aerated soil; otherwise, the rate of growth is considerably reduced.[75]

Response to the Aerial Environment.—The environmental factors that affect the root are not only those of the soil immediately about it but also those affecting the shoot. Through the shoot the root system is influenced by the aerial environment. The amount of light or the degree of humidity, temperature, etc., affects root development, by its effect upon food manufacture, water loss, and other activities of the shoot. Plants adapted to shade or diffuse light, when grown in full sunshine, develop better root systems and thus meet the greater transpiration demands. The effect of light on the growth of roots has been further demonstrated in the case of white-pine seedlings. Darkness induces the growth of tall seedlings with poorly developed roots; diffuse light, the growth of shorter plants and longer roots; and full light produces short, stocky plants with long, branching roots. For example, seedlings of similar age grown in a Vermont nursery under full shade had unbranched taproots 3.5 centimeters long. Those grown in half shade were 4.5 centimeters long and had the beginnings of laterals. Seedlings grown in

full light had taproots 5.2 centimeters long and a lateral development of roots nearly seven times as great as those in half shade. Among 50 seedlings excavated about 3 weeks later, the lengths of the root systems were 4.5, 8.2, and 13.8 centimeters and the total number of lateral branches 5, 143, and 468, respectively.[64]

RELATION OF ROOTS TO CULTURAL PRACTICES

Root distribution and development are greatly modified by various cultural practices, but our knowledge is very incomplete and a great deal more experimental work should be done in this field.

Transplanting.—Transplanting consists of lifting the plant from the medium in which its roots are established and replanting it in a different location. It is a violent operation, because the younger roots with their root hairs are, as a rule, torn away in the process of lifting. This is just the part of the root system that is most active in absorption. Taking up plants for transplanting results not only in breaking many of the roots but also especially in injury to the taproot. As a consequence, many new roots are formed. These do not grow so long as the original ones but form a more compact root mass about the base of the plant. Hence, the root system is less disturbed when the plant is finally transplanted into the field. Thus, although the root system of a transplanted plant may be less extensive than that of an undisturbed one, upon removal to the field the transplanted plant carries more roots with it and, consequently, more readily reestablishes itself (Figs. 127 and 128).

Nurserymen transplant trees and shrubs two or three times in order to force root development near the stem and thus to insure the preservation of more young roots when the plants are lifted for shipment. Hence, they have a better chance for recovery when again set out. This explains why nursery-grown trees and shrubs usually survive transplanting so much better than those secured from places where the roots have made their natural growth. Likewise, market gardeners find that transplanting young plants of cabbage, tomatoes, etc., while growing in cold frames, is a great advantage in assisting them to endure the final removal to open ground.

Effects of Transplanting.—Sow two flats of cabbage, tomatoes, peppers, or other easily transplanted crop. After 2 or 3 weeks, when the seedlings have the first pair of leaves well developed, transplant those from one flat to two similar ones, spacing the plants 2 inches apart. At the same time, thin those in the remaining flat so that they will be similarly spaced. Two weeks later, transplant the plants from one flat a second time, increasing the distance to 4 inches. After 2 weeks, determine (1) the effect of transplanting upon size of tops; (2) the amount of moist earth held by the roots when the plants are lifted with a trowel; and (3) the root development as shown by carefully washing away the soil and floating the roots out in water in black trays. To what are to be ascribed the differences obtained?

Transplanting is not beneficial in itself but only an expedient to grow plants out of their normal season or to give seedlings special care in cultivation, watering, protection from insects, etc. Experiments have clearly shown that the general effect of transplanting is to retard growth,

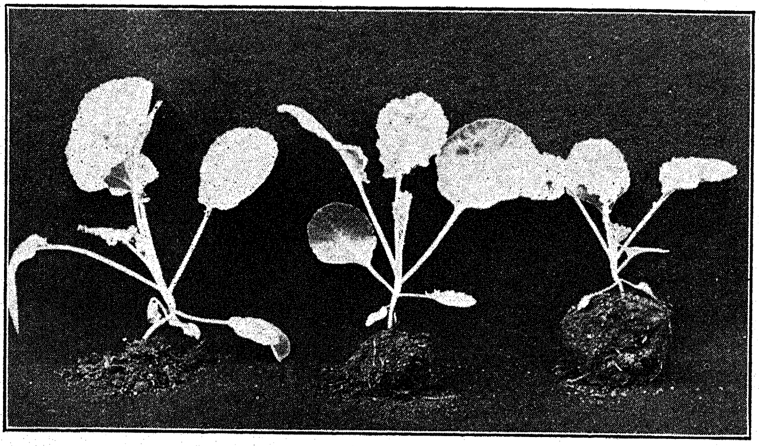

FIG. 127.—Cabbage seedlings not transplanted (left), and transplanted once and twice respectively. Note the greater amounts of soil held by the roots of those that were transplanted.

delay fruiting, and reduce yield. The degree of retardation varies with the kind of plant, its age, and the conditions of transplanting.

Certain species, *e.g.* cabbage, tomatoes, and beets, easily survive transplanting, others, such as peppers, onions, and carrots, are transplanted with more difficulty, and a third group consisting of corn, beans, melons, etc., are very difficult to transplant successfully even at an early age. Plants of the first group retain a relatively large proportion of their root system when transplanted, a fact due, in part, to their network

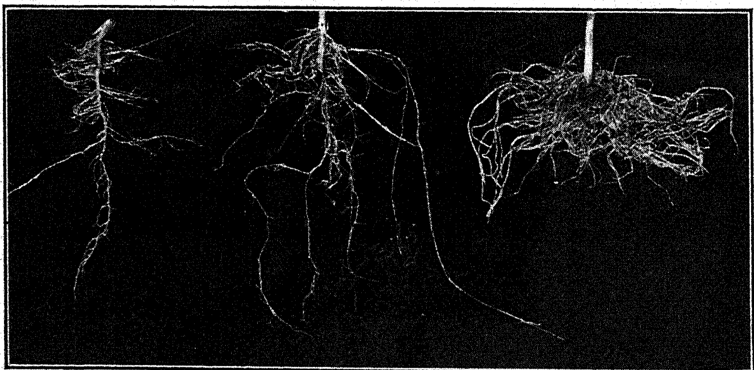

FIG. 128.—Roots of plants shown in Fig. 127.

of fine branches; the retained roots are much less suberized and, consequently, more efficient absorbers; and the rate of new root formation is much greater.[322] Obviously, the soil into which plants are transplanted should be in excellent tilth and brought into firm contact with the well-distributed roots.

In the transplanting of trees, both depth and spacing should be given careful attention. If the roots are placed either too deep or too shallow, the plant is at a decided disadvantage. Proper spacing in forest planting is necessary to obtain well-balanced and wind-firm root systems.[3] Orchard and shade trees as well as trees planted for windbreaks are not infrequently so closely spaced that insufficient room for proper root development results in a marked decrease or actual cessation of growth. The time of transplanting and of early spring cultivation should also be considered in relation to root development.

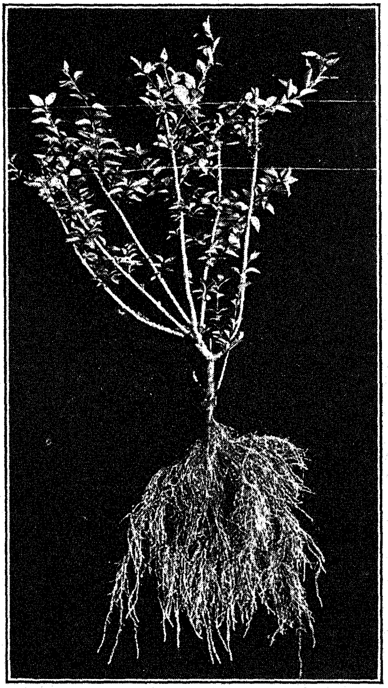

FIG. 129.—A properly pruned lilac (*Syringa*) about 6 weeks after transplanting. The stem is about 2 feet high.

Correlation between Root and Shoot Development.—The maintenance of a proper balance between root and shoot is of very great importance. If either is too limited or too great in extent, the other will not thrive. The root must be sufficiently wide spread to absorb enough water and nutrients for the stem and leaves, which in turn, must manufacture sufficient food for the maintenance of the root system. It is a well-established fact that grasses develop a better root system when they are undisturbed or mowed only once or twice a year than when they are closely and frequently grazed. In fact, one of the most important objects in the various systems of range and pasture management is to permit the seedling grasses to become well rooted before the tops are removed by grazing. Constant grazing starves the roots as does also too early and too frequent cutting of crops like alfalfa.[308,364] The absorbing area of the roots of winter wheat, exclusive of root hairs, increases rather uniformly with the transpiring area of the shoot and is constantly 10 to 35 per cent greater.[572]

In transplanting crops of various kinds, many of the roots of the young plants are necessarily destroyed. Hence, the top must be pruned

back or the plant protected from excessive water loss until the balance between the absorbing and the transpiring systems is reestablished (Fig. 129).

Pruning the tops retards root growth. Experiments with 3-year-old almond trees showed that the development of both the top and root system was inversely proportional to the severity of the pruning of tops The spread of the roots was over a third greater where pruning was light than where it was severe.[13] Pruning back the vines of sweet potatoes greatly reduces the yield as does also the practice of laying aside the vines in cultivation and not permitting them to develop adventitious roots.[175] In general, similar results are obtained by pruning the vines of tomatoes. The root system of a pruned tomato plant is reduced in about the same proportion as the top.[527]

Root Habits and Tillage.—Differences in growth and distribution of roots in the soil are responses to differences in physical and chemical conditions of the substratum in which they live. Tillage methods are a means of bringing about these changes. The depth of intertillage exerts a marked effect upon root habit and often upon yield. For the highest yields, cultivation should never be deep enough to injure the roots seriously. They should be allowed to occupy the richest portion of the soil, which is usually the furrow slice. The proper type of cultivation is deep enough to kill the weeds but shallow enough to reduce root injury to a minimum. A decrease of 2 to 8 bushels per acre in the yield of corn was brought about by deep cultivation in Illinois[588] and a decrease of 13 bushels in Missouri[232] (Fig. 130).

Extensive experiments with corn, cotton, and various garden crops have shown that the chief benefit of cultivation is derived from keeping down weeds which compete with the crop. Where weeds are few or absent, tillage is of little or no benefit. The roots of nearly all crops so thoroughly ramify the surface soil that little water is lost by direct evaporation. Cultivation, if at all deep, will destroy many of the roots and the plant will be unable to utilize the nutrients in this the richest portion of the substratum. When the roots are cut they usually branch more profusely.

It has been repeatedly demonstrated that mulching the soil and lack of tillage result in a marked growth of fibrous roots in the surface layers. Roots of fruit trees and other plants are often very superficial under a straw mulch. Irrigated trees under clean, shallow cultivation formed a thick mat of fibrous roots immediately below the soil mulch. Where they competed with grasses the roots were uniformly distributed to a depth of 2.5 feet.[8]

Depth of rooting can be controlled to a considerable extent by the use of cover crops or by intercropping. If the surface soil is depleted of its moisture by absorption, roots of both crops penetrate more deeply.

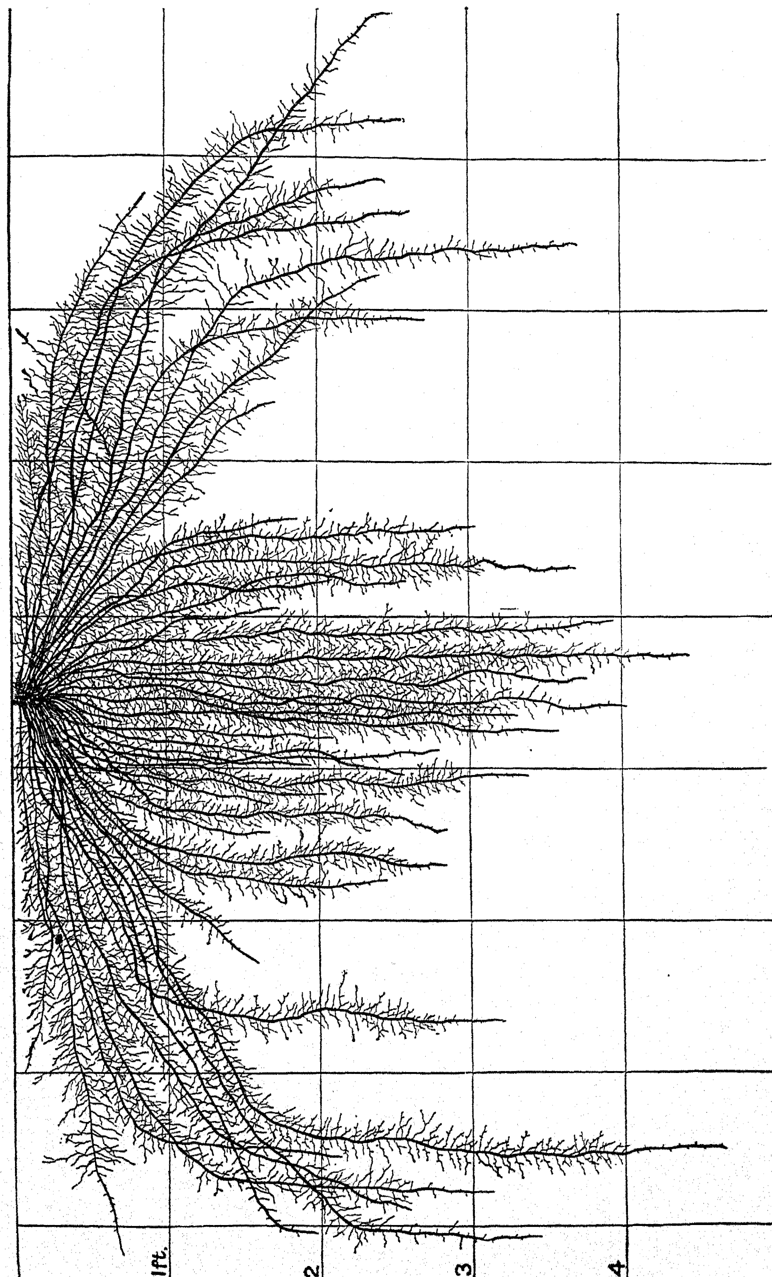

FIG. 130.—Root system of a corn plant 8 weeks old.

The effect that one kind of plant may have upon the root habit of another by modifying soil conditions is well illustrated in the case of chaparral and Monterey pine at Carmel, Calif. The trees growing in an open stand among the shrubs died when the latter were cleared away. A new growth of pine, however, flourished on the same area. The chaparral had shaded the soil and lessened evaporation from its surface, and the dense layers of rootlets and accumulated humus held the moisture in the surface soil. Consequently, the trees were shallow rooted and died of drought when the protecting cover was removed and the soil became desiccated. Seedling trees in the changed habitat evidently rooted more deeply.[72]

ROOT HABITS WITHIN THE COMMUNITY

Since each plant association has its own particular climate of which the water relation is usually the controlling factor, it is not surprising that these vegetational units often reveal marked differences in the general or community root habit of at least the dominant species. These are most fully known in certain grassland associations and in the southwestern deserts, although valuable information is also available in other communities including seral stages in the Rocky Mountains.

The plants of the tall-grass prairie of eastern Kansas, Nebraska, and Iowa have developed very efficient, widely spreading, and deeply penetrating root systems. The bluestems (*Andropogon*), tall marsh grass (*Spartina*), and wheat grasses (*Agropyron*) all have root systems which reach depths of 5 to 8 feet (Fig. 131). Those of June grass (*Kœleria*), wild rye (*Elymus*), and needle grass (*Stipa*) are less extensive, *i.e.* 1.5 to 4 feet. Many-flowered psoralea (*Psoralea*), wild licorice (*Glycyrrhiza*), ground plum (*Astragalus*), lead plant (*Amorpha*), and numerous sunflowers, goldenrods, asters, mints, roses, etc., are all deeply rooted. Frequently, the taproot and its major branches reach depths of 8 to 12 feet and depend little or not at all on the surface soil for moisture.

Of 43 species selected as typically representative of the tall-grass-prairie flora, only 14 per cent absorb almost entirely in the surface 2 feet of soil; 21 per cent have roots extending well below 2 feet but seldom beyond 5 feet; but 65 per cent have roots that reach depths quite below 5 feet, a penetration of 8 to 12 feet being common and a maximum depth of over 20 feet sometimes being attained.[562]

In this association there is sufficient rainfall to wet the soil very deeply, but it is not too wet for good aeration, while aerial conditions promote high transpiration. This results in very deep root penetration.

The roots of prairie species are grouped into about three more or less definite absorbing layers, many of the more deeply rooted species having few or no absorbing roots in the first foot or two of soil. The layering of the roots reduces competition and permits the growth of a larger number

of species. Little relation between layering and seasonal activity is apparent, however. The periods of most active growth and flower production of plants rooted at various levels occur synchronously.

On the hard-loam soils of the short-grass plains of western Nebraska and Kansas and eastern Colorado, a distinctly different type of community root habit occurs. Because of the low precipitation and high run-off, only the surface 18 to 24 inches of soil is regularly moist. Absorp-

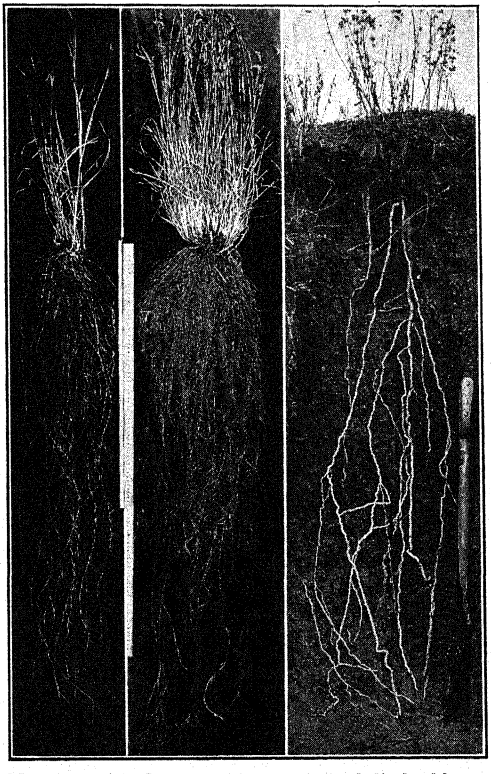

FIG. 131.—Big bluestem (*Andropogon furcatus*) and little bluestem (*A. scoparius*). The white lines are meter sticks, and the other plant is false prairie boneset (*Kuhnia glutinosa*), with roots often extending to a depth of 15 feet or more.

tion by the minutely and profusely branched fibrous roots of the dominant short grasses, *i.e.* blue grama (*Bouteloua gracilis*), buffalo grass (*Bulbilis*), Muhlenberg's ring grass (*Muhlenbergia gracillima*), and hairy grama (*Bouteloua hirsuta*), is confined usually to the surface 1.5 to 2 feet of soil (Fig. 132). This is true, also, for numerous annuals, and the cacti are notably shallow rooted, spreading many feet just beneath the surface of the soil (Fig. 194). All these species are well fitted to absorb vigorously following light showers, because of the widely spreading shallow roots, a character little in evidence in tall-grass prairie. Where, because of

run-in, rodent burrows, or sandier soil, water penetration is deeper, ground plum, loco weed (*Aragallus lamberti*), *Psoralea tenuiflora*, and a few other more deeply rooted species sparingly occur.

In the mixed-prairie association, where conditions are intermediate, dry soil often occurs at depths of 4 to 5 feet, and the short grasses penetrate more deeply. The roots of species common also to the tall-grass prairie are abbreviated in depth. This is usually correlated with the development of a more or less extensive surface-absorbing system.

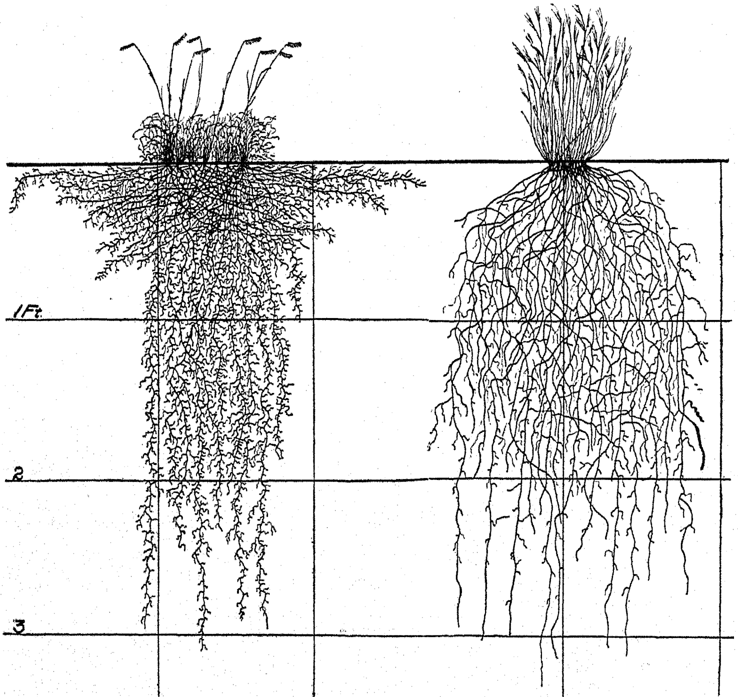

FIG. 132.—Blue grama (*Bouteloua gracilis*) and wire grass (*Aristida purpurea*).

Thus, the root habits are intermediate between those of tall-grass prairie and short-grass plains (Fig. 133).

The effect of soil type in relation to water penetration may greatly modify the kind of vegetation and depth of root penetration within an area of equal rainfall. In eastern Colorado, for example, under 17 inches rainfall, typical short-grass-plains conditions occur on hard-loam soils. But where the soil becomes more sandy, water penetration is greater and more deeply rooted grasses, *e.g.* wire grass (*Aristida*) and other species, become dominant. Where the substratum is nearly pure sand, run-off is practically nil, and water penetration reaches a maximum. Here the

very deeply rooted bunch grasses, *Andropogon hallii*, *A. scoparius*, sand reed (*Calamovilfa*), etc., dominate. Many other very deeply rooted

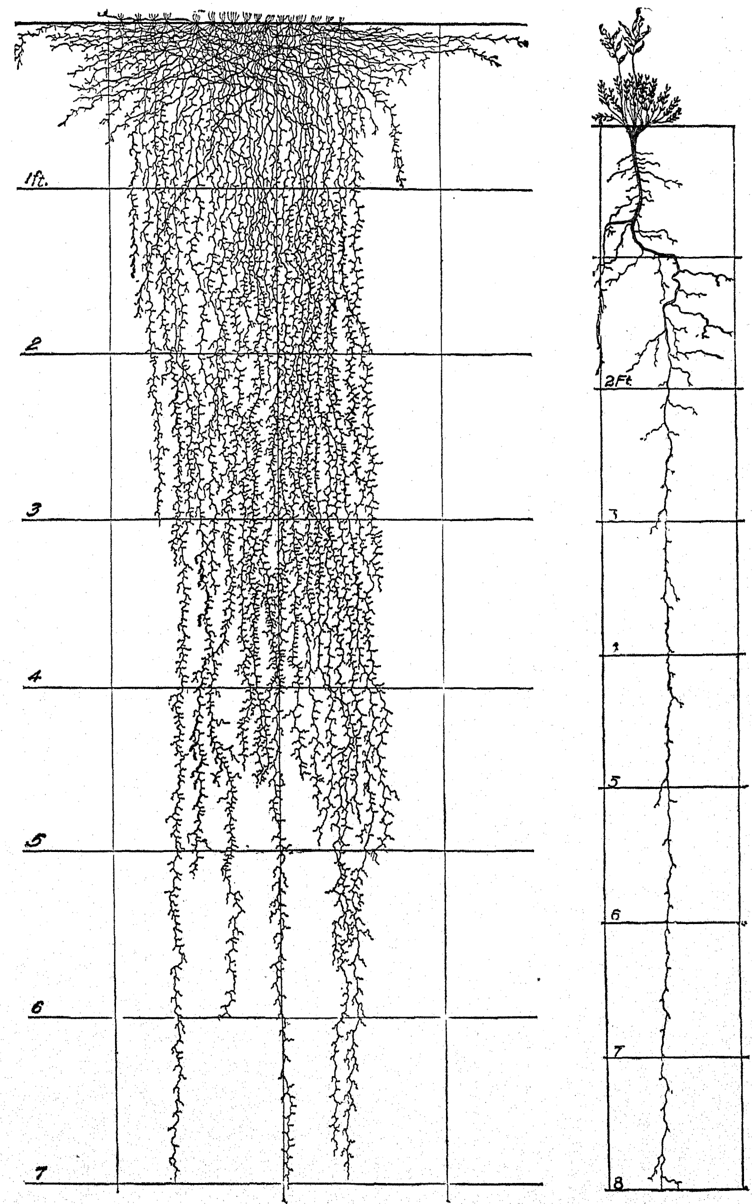

FIG. 133.—Buffalo grass (*Bulbilis dactyloides*) and loco weed (*Aragallus lamberti*) in mixed prairie.

herbs also occur, both vegetation and root habit being markedly different from that on sandy-loam soil (Fig. 134).

The Palouse (*Agropyron-Festuca*) prairie of the Pacific Northwest grows under a moderate winter and low summer precipitation of about 23 inches annually. The silt-loam soils are usually deep and have a high water-retaining power. In early summer, the surface-soil layers lose all of their available water, a fact indicated by the early maturing of the dominant, *Festuca ovina*, and certain other shallow-rooted grasses (Fig. 116). As the season advances, drought occurs in the deeper soil, the subsoil usually being quite thoroughly depleted of its moisture. Wheat bunch grass (*Agropyron spicatum*), another dominant, matures early, dries out in July, but renews growth upon the advent of the autumn rains. Little provision is made for absorption in the surface soil, the root system penetrating to about 4 feet. Many of the other species absorb in the first 4 to 6 feet of soil; a few penetrate more deeply. Nearly all mature by midsummer, late-blooming grasses being noticeably absent.

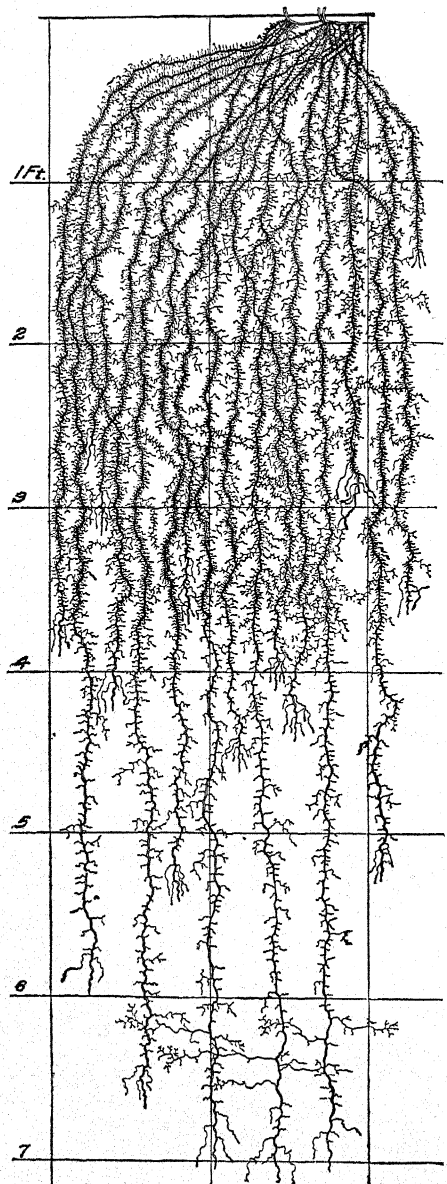

Fig. 134.—Root system of sandhill bluestem (*Andropogon hallii*).

Under the same Great Basin type of rainfall but where it is only 16 inches or less in amount and falls upon a deep, pervious soil, conditions are less favorable for the growth of grasses. Here the vegetation constitutes the *Artemisia-Atriplex* or Basin sagebrush association. The sagebrush (*Artemisia tridentata*) has a taproot system which branches widely and penetrates to a depth of 5 to 11 feet. It also has a highly developed system of laterals for absorption in the shallower soil (Fig. 135). Shadscale (*Atriplex confertifolia*) is likewise well provided

with a root system excellently adapted to absorb both in the shallow and in the deep soil. These dominants are illustrative of many other shrubby, half shrubby, and perennial, herbaceous species of the Basin Desert.

Root systems of annual plants in the desert scrub association, *e.g.* about Tucson, Ariz., are all quite shallow. Most of them do not penetrate to depths greater than 8 inches. Here the precipitation is only about 11 inches annually and there are two rainy seasons, one in summer,

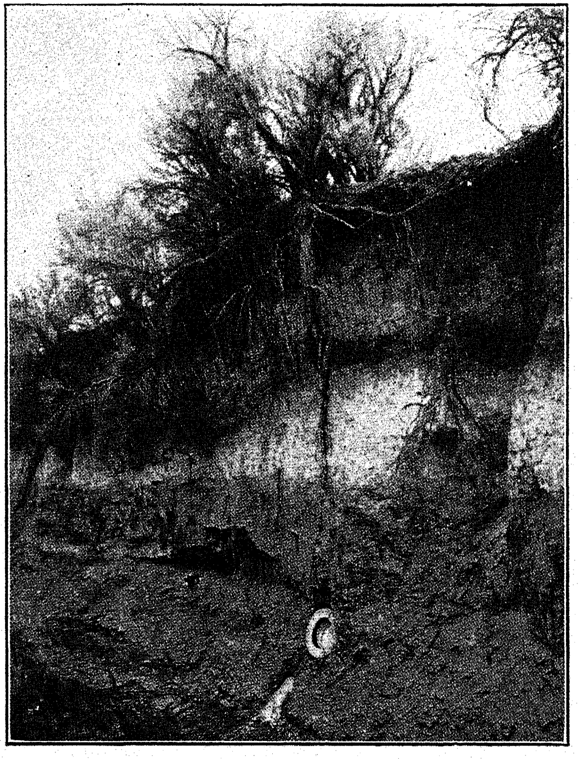

Fig. 135.—Sagebrush (*Artemisia tridentata*) showing generalized type of root system with deep taproot and widely spreading laterals many of which are in the surface soil. (*After Kearney, et al.*)

another in winter. Winter annuals are, in general, characterized by a prominently developed taproot and a meager development of laterals. Roots of summer annuals penetrate to about the same depth, but the lateral branches are much more prominent and the total absorbing surface greater. This is apparently correlated with the more rapid growth and greater transpiring surface of the latter. The perennials have three types of root systems: (1) the generalized type, where both taproot and laterals are well developed (*e.g.* creosote bush, *Covillea* and mesquite, *Prosopis*); a specialized type (2), with strong development of taproot and few

branches, such as *Ephedra*, or (3), with laterals very highly developed, as in most cacti. On the upland the roots do not penetrate, as a rule, deeper than 12 inches, the depth of available soil. Those on the flood plains reach depths of 6 to 16 feet or more. Perennials with the generalized type of root system have the widest local distribution, and those with the pronounced development of the taproot have the most limited. In general, there is a tendency to form three layers of roots in the soil, the uppermost of annuals, followed closely by the root layer of cacti and a much broader, deeper-seated layer composed of taproot systems with or without prominent laterals. The wide spread of laterals in many of the dominants explains the characteristic open spacing of the desert scrub and the bush-like habit.[71]

Little is known of the root penetration of mature trees in forests.[404] It seems very probable, however, that under the relatively high rainfall necessary for the development of deciduous forests, for example, the subsoil is often quite too moist and consequently too poorly aerated for deep root penetration. Both the shade from the forest cover and the surface mulch of litter, moreover, tend to prevent evaporation and promote the thorough occupancy of the surface soil by roots. It seems probable that the bulk of the roots of the plants of the deciduous forest may occur in the surface 1 to 3 feet, but where the trees grow on well-drained uplands much greater depths are attained.

A Study of the Root Habits of Plants.—A thorough study of the entire root system of even a single plant is usually a laborious, time-consuming process,[566] but many facts of ecological interest and importance may be learned in the course of the regular field work. A spade and hand pick, one end of which is drawn out to a sharp point, and an ice pick should be a part of the field equipment. Examine and compare the relative coarseness or fineness of the roots of grasses which are adapted to low, moist soil and dry, upland soil, respectively. Follow the rhizomes of various sod-forming grasses and ascertain the distribution of the roots upon them. Examine the underground parts in the surface soil of various herbaceous species that form dense societies. Study the nature of the shallower roots of various legumes, composites, etc. Do all absorb in the surface soil? The roots of seedlings should also be examined, especially those of trees. Do they show any adaptations to thrive in moist or dry soil? Examination of the roots of beech, oaks, etc., will reveal an intimate fungus-root relation known as mycorrhiza (p. 252). In freshly cut banks along roadways, railway cuts, eroding streams, etc., it is usually possible to examine root penetration and distribution to great depths. Are the native plants of your region deeply rooted? Can you discover to what depths various field and garden crops penetrate and how widely the roots spread?[568] What factors are concerned in the behavior in different habitats?

ROOT HAIRS AND FACTORS AFFECTING THEIR DEVELOPMENT

The formation of root hairs in plants possessing them is apparently not a morphological necessity, as are other organs or tissues, but seems to be related to the direct influence of some factors of the environment,

especially water content and oxygen supply.[77] Some aquatic angiosperms and several gymnosperms such as the firs (*Abies*), redwood (*Sequoia*), and Scotch pine (*Pinus sylvestris*) produce no root hairs. On the other hand, certain plants that grow in very dry places (*e.g.* piñon pine) produce root hairs that have thick, lignified walls, that persist for several months or even years.[579] Others such as redbud (*Cercis canadensis*), honey locust (*Gleditsia triacanthos*), Kentucky coffee tree (*Gymnocladus dioica*), as well as a rather large number of composites, have root hairs of several years' duration.[340] It seems probable that in all of these cases the habit of producing thick-walled root hairs was formed at a time when these species grew only in very dry situations.

In roots that are permanently hairy, the root-hair zone may be general or limited to either the distal or proximal region of the root. Where root hairs persist in either herbs or trees, there is little or no secondary thickening of the root. In most plants, the initiation of a layer of periderm or cork marks the end of absorption, but this begins to form only after the root hairs cease to function. In the roots of most grasses, both the epidermis and fleshy cortex may slough off, except the innermost layer or endodermis. It becomes cutinized or suberized and the roots appear dead. The deeper portions, however, are clothed with root hairs that are absorbing vigorously, although the older portion of the root system is serving merely for anchorage and conduction.

The absorbing area of the root is greatly increased by the growth of root hairs. For example, in the case of corn it has been calculated that the area is 5.5 times that of a hairless root of similar size; in garden peas, 12.4 times, and in certain other plants, as much as 18 times.[455] It is not surprising, therefore, that the amount of water and air in the soil has a marked effect upon the development of root hairs. The root-hair zone, though often only a few millimeters long, may extend through distances of many centimeters, especially on rapidly growing plants in moist soil. The length of life of an ordinary root hair is, in part, moreover, dependent upon the environment. In dry soil it is shorter; in well-aerated, moist soil, of longer duration; and the root-hair zone may be 2 or more feet in length. Both air roots and water roots are commonly without hairs, although root hairs on some plants are readily produced either in a saturated atmosphere or in an aqueous medium provided that calcium is present in the latter.[158] Hairs are more abundant, even in the same species, in soil beneath flowing water than where the water is standing. This is in accord with the fact that oxygen is necessary for the development of root hairs, and their usual absence or weak development in ponds or swamps is due, in part, to low oxygen content. In moderately moist soils, the roots of many plants are almost woolly with root hairs, there are fewer in wet soil, and usually none in water. Of course, if soils become very dry, both root hairs and young

rootlets die. Root-hair development may also be retarded by a very concentrated soil solution such as occurs in alkali soils. Extremes of temperature are also inimical to their growth. They develop in the light and dark about equally well, provided there is ample moisture.[263,501]

The intimate contact of root hairs with the water and solutes that form a film around the soil particles is due to the presence of mucilaginous materials in the outer lamella of the wall, which in some plants has been shown to be pectin mucilage.[252,411] Hence, the high efficiency of root hairs as absorbing organs. The osmotic concentration within the root hairs varies with the medium in which they grow. It is least where water is abundant, often only 3 or 4 atmospheres. This, however, is much greater than the osmotic pressure of the soil solution which is only 0.2 to 1 atmosphere in ordinary agricultural soils. Osmotic pressure within the root hairs increases as the soil becomes drier or in plants adapted to dry and especially saline habitats to many times that amount.[238] The osmotic pressure may, moreover, be increased by increasing the rate of transpiration.[257]

UNDERGROUND STEMS AND ROOT OFFSHOOTS

Aside from absorption and anchorage, other activities of underground plant parts are storage and propagation. Vegetative reproduction is very largely by stems of which the commonest and most efficient type is the rhizome, although tubers, bulbs, corms, and root offshoots also play an important part (Figs. 136 and 137). These same organs are frequently enlarged and serve for food accumulation, especially in perennial herbs, where the aboveground parts die at the end of the growing season. These underground parts are not confined to plants of a particular habitat but occur widely in swamps, woodlands, grasslands, and sandy wastes. Usually, however, they are larger and thicker, especially rhizomes, in species inhabiting swamps or moist soil and finer and often shorter in harder or drier soil.

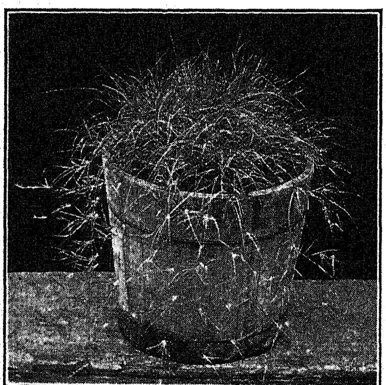

FIG. 136.—Propagation by stolons, buffalo grass (*Bulbilis*).

Some rhizomes may compose the entire stem system, *e.g.* various violets and most ferns, in which case they give rise to aerial leaves, but in most cases they bear only scale leaves. They may be simple or only slightly branched, as in Solomon's-seal (*Polygonatum*) and certain rushes (*e.g. Juncus balticus*). Each season the younger portions extend

a few inches forward, the older parts frequently decaying. This gives rise to *linear migration* by which the plant invades new areas. Where several shoots develop each year, the line of migration is clearly evident (Fig. 76). More commonly, rhizomes are greatly branched and grow in all directions from the parent area. The result of this *radial migration* is to form more or less symmetrical communities, the central portions of which may be unoccupied by the particular species. The decay of the older portions in branched rhizomes results in the multiplication of individuals. This, however, is not so important as the advance into new territory.

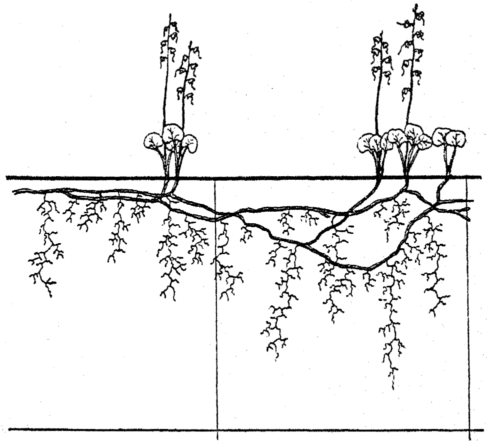

FIG. 137.– Propagation by underground stems, wintergreen (*Pyrola chlorantha*).

By means of rhizomes and root offshoots, plants may invade closed communities, such as grassland, where propagation by seeds or stolons would be difficult or impossible. It is in this effective manner that many shrubs and half-shrubs extend their area of occupation, *e.g.* coralberry (*Symphoricarpos*), hazelnut (*Corylus*), rose (*Rosa*), ninebark (*Opulaster*), etc. (Fig. 64). The rhizomes of sumac (*Rhus glabra*) are often 25 feet long. Various species of willows, poplars, plums, and the Osage orange spread widely by means of root offshoots.

Many of the longest and best developed rhizomes are found among plants growing in loose, sandy soil. Here the elongated, sharp-pointed buds penetrate the substratum with ease. In general, rhizomes grow parallel to the soil surface at a depth of a few inches, varying with the species. Where they are covered with shifting sand the rhizomes ascend, sometimes vertically, giving off roots abundantly. When soil is removed they descend to the proper level. Thus, the surface 1 to 2 feet of sandhills or dunes may contain a tangled mat of rhizomes and roots of sand-binding species, especially grasses. In *Redfieldia* the much branched stems are frequently 20 to 40 feet long and sometimes buried 4 feet deep (Fig. 138).

Sod-forming grasses, carices, and rushes, *e.g.* bluegrass, sedges, spike rush, etc., have the rhizome habit well developed. But in bunch grasses like orchard grass, certain wheat grasses, etc., the stem grows up parallel with the parent culm until it emerges from the axillary sheath. Some species, such as little bluestem, form a sod under favorable conditions of

water content but resort to the bunch habit where the soil is dry. Many goldenrods, sunflowers, yuccas, asters, mints, and sages migrate by means of rhizomes. Certain species like buffalo grass and snowberries spread by both stolons and rhizomes.

In bogs, because of little mechanical resistance, the underground parts are remarkably straight, and in both bogs and swamps the depth of penetration is often limited by the water level. The thick, coarse rhizomes of cattails, arrowheads, swamp reed, great bulrush, etc.,

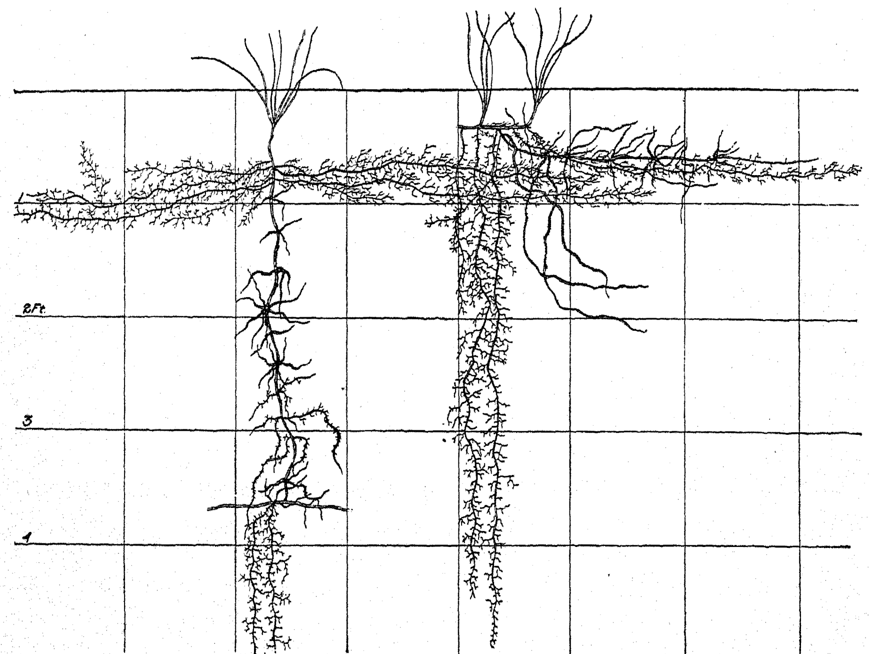

FIG. 138.—Rhizomes and roots of *Redfieldia flexuosa;* the plant on the left has been buried to a depth of nearly 4 feet.

however, grow at depths of 3 to 12 inches, often below the water table.[154] Such rhizomes, like roots which grow below water, are very rich in aërenchyma. Stems of certain woody species, such as water willow (*Decodon*), produce aerenchyma upon coming in contact with water, but most woody species such as willows, birches, and alders have little or none.

The hollow rhizomes of *Phragmites* occur from near the soil surface often to a depth of 18 inches. Those of *Typha*, *Sagittaria*, and *Polygonum* occupy the soil at various levels. Differences in the depth of rhizomes in swamps and the degree to which they occupy the soil have led to classification into competitive and complementary communities. Since there is still much unoccupied space, and no competition for water

or dissolved nutrients (although air may be deficient), light and not room underground appears to be the controlling factor.

Although tubers, corms, and bulbs are excellent organs for food accumulation and protection of growing points during cold or drought, they are much inferior to rhizomes as organs of propagation. This is because of their slight elongation and consequent lack of migration.

SOIL ORGANISMS

The soil is not a mass of inert inorganic material. It is the home of countless billions of microorganisms—bacteria, fungi, algæ, and Protozoa—which throng its dark passageways. Earthworms, insects, etc., and numerous burrowing animals find in it food or shelter. A single gram of loam from the surface soil may contain 14,000,000 to 58,000,000 bacteria, and in some soils even at a depth of 3 feet, as many as 37,000 per gram have been found.[59] The mycelia of fungi ramify soils, especially those rich in humus. The toadstools and puffballs of forest and grassland are most conspicuous, but hundreds of species of smaller, mold-like forms occur in countless numbers. Algæ are frequently abundant. Protozoa are common in many soils, and sometimes a gram of soil may contain as many as 10,000 to 2,000,000 individuals. Many of these feed chiefly upon soil bacteria.[419]

The Relation to Nitrogen.—Among this vast assemblage of dwellers in the soil, certain groups deserve especial mention, since they are concerned very directly with the supply of nitrogen, a constituent of the protoplasm and a substance most indispensable to plants. The ammonia liberated in the breaking down of proteins, a process called *ammonification,* is oxidized to nitrites by certain kinds of bacteria (*Nitrosomonas* and *Nitrosococcus*). The nitrites are further oxidized by other bacteria (*Nitrobacter*) to nitrates, which is the form of nitrogen most favorable for green plants. The process of nitrification is exceedingly important since plants can not use nitrogen from the abundant supply in the air but must rely entirely upon compounds absorbed in solution through the roots. Hence, the presence of mineral salts containing combined nitrogen is a factor of great importance in soil productiveness. Since the supply of nitrates is constantly diminished by leaching and absorption by plants, its renewal is imperative.

Several species of soil bacteria functioning independently of higher plants possess the power of taking the free nitrogen from the air and incorporating it into organic compounds. In this way, much nitrogen is added to the soil. A gain of from 25 to 40 pounds per acre per year has been determined by different investigators. Both nitrifying and nitrogen-fixing bacteria thrive in the humus, and it is largely due to their activities that soils containing much humus are so productive.

Nitrifying and nitrogen-fixing bacteria, like all other soil organisms, are profoundly affected in their activities by the environment. Acidity of the soil has an important effect upon bacterial processes. It may increase to such a point that the decomposition of plant tissues is hindered, a layer of peat being formed similar to that developed under poor aeration. The degree of acidity that is toxic varies greatly with different species, nitrifying and nitrogen-fixing bacteria being very intolerant of acidity. Extreme alkalinity is also detrimental. The water content of soil and the temperature likewise exert a profound effect. Most soil bacteria do not become active until temperatures of 45° to 50°F. are attained. In one experiment, the amount of nitric nitrogen produced per acre in a period of 3 weeks was 3.6 pounds at 44°F., 17.8 pounds at 78°, 46.6 pounds at 94°, but only 10.8 pounds at 111°. Under favorable temperature, only 2.8 pounds were formed in dry soil and 8.2 pounds in one of medium water content, but 29.6 pounds per acre during a similar 3-week period where the water content was very favorable.[417] Much larger quantities are, moreover, produced in rich than in poor, eroded soils.

Among certain plants, notably the legumes, which are very rich in nitrogenous compounds, a close relationship exists between other species of nitrogen-fixing bacteria and the roots. Here, the bacteria are found in the root nodules as on clovers and alfalfa. From 40 to over 250 pounds of nitrogen per acre may thus be added to the soil in a single season through the activities of these bacteria. This explains why the practice of growing leguminous crops and plowing them under as green manure has such a stimulating effect upon the growth of succeeding crops. The occurrence of legumes and other nodule-bearing plants among native vegetation is undoubtedly of great significance in maintaining soil fertility. They reach their best development in neutral or nearly neutral soils which are not too rich in nitrates.[186]

Experiments with the development of nodules on legumes have shown that they become much larger when soil temperatures are most favorable. In the soy bean, a consistent increase in dry weight of nodules occurred as the soil temperature increased from 15° to 24°C. At higher temperatures, a progressive decrease occurred. Alfalfa, red clover, and field peas likewise gave a maximum nodule production at a soil temperature of about 24°C.[273]

Relation to Disease.—The soil factors exercise a strong influence upon the development and expression of disease.[270] Many diseases, such as chlorosis of tobacco, pineapple, coniferous seedlings, etc., are due to the deficiency or unavailability of sufficient magnesium or iron.[294] Yellow berry of wheat is caused by a low available supply of nitrogen.[268] Potash hunger of potatoes results in discoloration of the foliage, wilting, etc. Disease may be caused by an excess supply of nitrates, calcium, or magnesium salts or a disturbed water or air relation. Blossom-end rot of

tomatoes, for example, is due to drought, and straight head of rice probably to poor aeration. Soil temperature is an extremely important environmental factor since it has a marked effect upon disease-producing organisms.

Frequently, the influence of environmental factors on the host seems to be the fundamental cause of susceptibility to disease. Proper soil and other conditions for a vigorous development of root and shoot are desirable. Corn and wheat seedlings, for example, are sheathed at the outset with protective coverings, chiefly of pectic substances, through which invasions of soil organisms may rather easily take place. But in normally balanced seedling development, the cell membranes of the protective coverings pass quickly to a condition of maturity where celluloses and even lignin or suberin predominate. Thus, because of

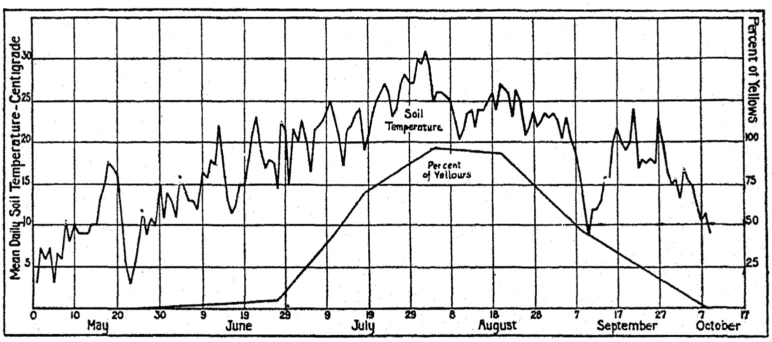

FIG. 139.—Graphs showing the relation of temperature to the development of cabbage yellows. (*After Jones, et al.*)

chemical changes in the cell walls, the tissues which were subject to invasion change rapidly so that they become relatively resistant. The soil and air temperatures that promote this normal balanced seedling development vary with the crop. In the case of wheat, for example, they are low, but in corn, much higher.[142,143]

It has been clearly demonstrated that many soil-borne diseases are conditioned in their occurrence by the factor of soil temperature. Cabbage yellows,[271] flax wilt,[535] tomato wilt,[85] and tobacco root rot[266] are examples of diseases caused by soil-inhabiting fungi gaining entrance to the host plant through the root system. In each case, the disease has been experimentally developed in destructiveness ranging consistently from 0 to 100 per cent of the crop by changing the single factor of soil temperature.[270] The temperature ranges employed were well within those reasonably congenial to the respective hosts (Fig. 139). For example, flax wilt, which, like the wilt of cabbage and tomato, is favored by a high temperature, gives extreme development of disease at 24° to 28°C. but none above 38° or below 14°C.[274] Conversely, tobacco root-rot

development is favored by lower soil temperatures, the most favorable range being between 17° and 23°C.[266]

The regional distribution of a plant disease is sometimes determined by temperature. The presence of onion smut, for example, is dependent upon the soil temperature during the seedling stage of the growth of the host. Infection and development of smut are favored by relatively low temperatures and inhibited by high ones, with 29°C. as approximately the critical point. Hence, though common in the North, it is almost unknown in the South, although annually introduced with Northern-grown bulbs.[550] In the Pacific Northwest, soil temperatures of 0° to 5°C. are decidedly unfavorable to successful infection of wheat by stinking smut. This holds, also, for temperatures higher than 22°C., while 15° to 22° are optimum for its development.[269]

The soil reaction often exerts a controlling effect upon disease-producing organisms. The slime mold (*Plasmodiophora brassicæ*), which produces clubroot of cabbage and other crucifers, is most injurious in acid soils. By the addition of lime, the soil becomes a more favorable habitat for the roots of the host but much less so for the parasite. The fungus (*Gibberella saubinetti*) producing wheat scab does little or no harm at pH 5.5. A potato-scab fungus (*Oospora*) is less tolerant of acid soil than is its host. Consequently, potatoes can be grown well in certain soils and remain entirely free from attack. Some of the most important problems of plant pathology deal with the relation of environmental factors to the occurrence and severity of disease.[249]

Mycorrhiza.—In many plants such as the pines, oaks, orchids, and many ericads, fungi are habitually associated with the roots.[339,341] A mycorrhiza (*i.e* fungus root) is a structure composed of root and fungus. If the fungal mycelium occurs on the outside of the root and between its cells, as on many oaks, hickories, pines, beech, etc., the mycorrhiza is ectotrophic (*i.e.* nourished outside). In endotrophic mycorrhiza (*i.e.* nourished within), as in red maple (*Acer rubrum*), orchids, many *Ericaceæ*, etc., the fungus occurs inside the root where certain cortical cells usually contain closely interwoven clumps of hyphæ which often enfold the nucleus. The root hairs, which are usually sparse, may also be filled with hyphæ [406,407] (Fig. 140).

Ectotrophic mycorrhizas are caused by many kinds of fungi, those on forest trees apparently always by Basidiomycetes, many having been synthesized experimentally.[348] The hyphæ of the mushroom penetrate the outer cell wall of the rootlet and often split it by dissolving the middle lamella. It then continues to grow until it develops a fungus mantle which completely envelopes the rootlet. Simultaneously, branches of the mycelium penetrate between the outer cortical cells of the rootlets, causing the walls to split and the cells to be pushed apart. Since further elongation of the rootlet is inhibited by the fungus mantle

excessive branching is induced. The branches also are soon infected and covered by the fungus, and, consequently, most plants showing a good development of mycorrhiza have roots that are short and thick and present a coral-like appearance (Fig. 141).

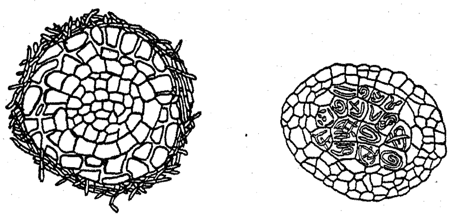

Fig. 140.—Cross-section of ectotrophic mycorrhiza on red spruce (*Picea rubra*), and an endotrophic mycorrhiza on red maple (*Acer rubrum*). (*After McDougall.*)

They vary in color, depending upon the kind of fungus, from white to bright yellow, brick red, or dark brown. They usually occur only in the upper layer of humus-filled soil on the smallest rootlets, the hyphæ composing the fungal root mantle connecting with the mycelia that permeate the humus. A single tree may show three or four kinds

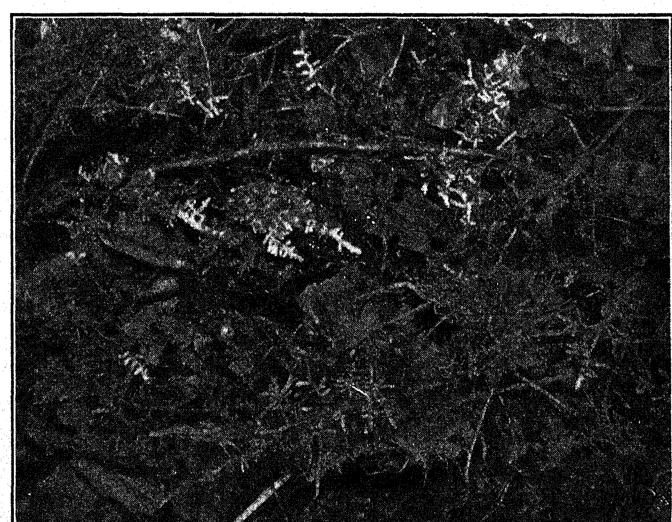

Fig. 141.—Ectotrophic mycorrhiza on the hornbeam (*Carpinus*) in leaf mold. (*Photo furnished by W. B. McDougall.*)

of mycorrhizas differing in form, size, color, and texture, but each is due to a different fungus. More usually, only a certain species of fungus appears always to be associated with a particular tree species Only a small portion of the root system may exhibit mycorrhiza, but here root hairs are few or wanting, or, at the other extreme, as in the Indian pipe (*Monotropa uniflora*), the entire root system is compacted

into a clump of fungus mycelium and does not come in contact with the soil at all.

Endotrophic mycorrhizas are best known in the *Orchidaceæ*, *Ericaceæ*, and *Gentianaceæ*.[405] The rootlets containing the fungus are sometimes transformed into bead-like galls. In most cases, the fungi concerned are apparently not Basidiomycetes but microscopic molds, for the most part not well known. Apparently, they are specialized forms rather than ordinary soil fungi. Many orchids are entirely dependent upon mycorrhizal fungi. Under natural conditions, the seeds of some orchids do not germinate unless infected by mycorrhizal fungi, although germination may be brought about artificially by the addition of appropriate culture media, *e.g.* those containing fructose. In other species, the seeds germinate but do not develop beyond the seedling stage unless they become infected with the proper kind of fungus. Orchid roots are characteristically fleshy and tuber-like. They differ much more from ordinary roots than those associated with ectotrophic fungi. Some plants, as *Corallorrhiza* and *Epipogon*, have no roots, the underground parts consisting entirely of branched, fungus-infested rhizomes. Endotrophic mycorrhizas are common also among the *Ericaceæ*, certain genera such as *Vaccinium*, *Calluna*, and *Rhododendron* being more or less dependent upon mycorrhizal fungi. Since the fungi can grow only in an acid substratum, these higher plants can flourish only in an acid soil.

Distribution and Significance.—Mycorrhizas are of extremely wide distribution and of common occurrence. Mycorrhizal fungi have been recorded for every group of chlorophyll-bearing plants except the algæ. Even the cultivated cereals have been added to the constantly growing list. In Germany, 70 out of 105 species taken at random had root fungi, and in Java 69 out of 75.

As would be expected, mycorrhizas are associated abundantly with plants rooted in forest mold. They are rare in water and wet soil, except in bogs where organic matter is abundant. They are especially common on bulbous and tuberous plants. In the Great Lakes and deciduous forests mycorrhizas are abundant, as they are also in the Pacific Coast forests, but in the central Rocky Mountain region they are less numerous.[342]

Many investigators consider the relation of the fungus to higher plants one of parasitism, a relationship which seems clearly evident in some cases, such as certain orchids. On the other hand, some higher plants, *e.g.* the colorless *Monotropa uniflora*, appear to be parasitic upon the fungus. It would be entirely unsafe to generalize, but much experimental evidence points to the conclusion that among many species and particularly coniferous forest trees, mycorrhizas exhibit a symbiotic relationship.[348] Experimental evidence supports the belief that the fungus appropriates carbon compounds from the green plant and may

also be benefited by certain other substances, for example phosphorus. On the other hand, it is well known that nitrates are low in forest humus, particularly if the reaction is acid. In such acid soils, where the nitrogen supplies exist in the form of organic compounds of relatively complex type, coniferous mycorrhizas abound. Experiments show that on such soils tree growth with mycorrhiza is much greater than without, the fungi making the nitrogen readily available for the trees. The fungi, moreover, apparently absorb certain salts more readily than do root hairs. Thus, it seems that mycorrhizas possess a vital significance for trees and other plants, especially those growing in acid humus. This is a field of ecology deserving much further study.

CHAPTER XI

HUMIDITY, WIND, AND EVAPORATION

The chief factors of the aerial environment of plants are humidity, light, temperature, and wind. All are much more subject to rapid fluctuations than are the factors of the soil. As in the soil, an extremely important environmental relation is that of water. The amount of water vapor in the air is one of the chief factors influencing vegetation.

HUMIDITY

The moisture of the air which is in the form of vapor is termed humidity. It is one of the most important factors since it directly affects the rate of transpiration. The amount of water that a plant loses frequently determines whether it can or can not grow in a given habitat. Owing to the nature of the medium in which it occurs, water vapor is much more uniformly distributed than is the water in the soil. For the same reason, it fluctuates to a much greater degree. It differs from soil water also in that a part of the latter, *i.e.* the echard, is always non-available to the plant, while the whole humidity of the air is the external stimulus that controls the water loss from the shoot.

The actual amount of water present in the air is called the absolute humidity. It is expressed in grains per cubic foot of air. It is not so important as the relative amount, since the latter determines whether the climate of a place is physically moist or dry. Even in a desert, the absolute humidity may equal or exceed that in a region usually considered moist.[283] The relative humidity is the ratio of the water vapor present in the air at a certain temperature and pressure to the amount necessary to saturate it under these conditions. For example, 50 per cent relative humidity means that the air contains one-half the amount of water vapor necessary to saturate it (100 per cent). The lower the relative humidity the more rapidly the air will take up water from the transpiring leaf or from a moist soil surface.

Modifying Influence of Temperature and Wind.—Humidity is affected by temperature, wind, pressure, altitude, exposure, cover, and water content. High temperatures increase the capacity of the air for moisture and consequently lower the relative humidity. At low temperatures, the air will hold less moisture and consequently its relative humidity is increased. This accounts for the increased precipitation with altitude on the windward sides of mountain ranges of moderate

elevation where the ascending air currents are cooled. For example, in the alpine meadows at the summit of Pike's Peak, 14,100 feet altitude, the annual precipitation is 30 inches. In the subalpine forest at 10,200 feet, it is 25 inches but decreases to 22 inches in the montane forest at 8,500 feet and to only 15 inches on the treeless plains at the foot of the mountain.

The air in a room 20 by 20 by 10 feet, if completely saturated at 80°F., contains approximately 3 liters of liquid water in the form of vapor. But at 60° it could hold only half this amount, and at 0° only 0.15 liter. Hence, of two regions, or two habitats with the same rainfall, the warmer is the drier. During the day, the relative humidity falls as the temperature increases and rises in the evening as the air grows cooler. Each change of a degree Fahrenheit in temperature usually produces a corresponding variation, but in the opposite direction, of 1.5 to over 2 per cent humidity, depending upon the locality.[283] The air may become saturated with water and moisture may be precipitated out as dew even during dry weather if the night temperatures are sufficiently low. With a given amount of water vapor in the air, transpiration from plants and evaporation from the soil are increased with a rise of temperature through the effect of the latter upon humidity.

Wind has a powerful effect upon humidity in that dry winds lower the amount of air moisture by removing the moist air about plants and mixing it with dry air. This has the effect of keeping the immediate humidity low and promoting transpiration.

Since the velocity of the wind increases with the height above the soil surface, trees especially suffer from the drying effects. Low-growing vegetation such as rosette and mat forms are much less affected. Transpiration is often so greatly increased and growth so much retarded on the windward side of trees, that the larger part of the exposed crown is on the leeward side. In prairie-planted groves, for example, the drying effect of southwest winds results in the dwarfing or death of the trees on the exposed sides of the grove, the protected trees attaining a much greater height.

The height to which many plants can attain is limited by their ability to absorb and transport water upward rapidly enough to replace that lost through transpiration. On wind-swept coasts and on high mountains, excessive water loss results in a stunted and gnarled growth.[522] This is, however, partly due to the mechanical effect of the wind. The gnarled, sprawling, much-branched, elfin timber grows through the short summer of high altitudes in cold soil from which it is difficult to absorb and under the drying effect of high winds (Fig. 142). So adverse are the conditions of the environment that trees several hundred years old may be only a few inches in diameter and attain a height of only a few inches or, at most, a few feet. Similarly, in Arctic regions, because of

winterkilling due to drought, willows, alders, and other woody species, instead of growing erect, develop the sprawling or espalier shape, parts not covered by snow in winter being regularly killed back. Practically all, moreover, of the herbaceous species are long lived and have their resting buds protected by the surface soil. Herbs, too, may form a one-sided growth or take on a prostrate habit, form cushion-like clumps, and, in extreme cases, may be confined to depressions.

The drying effect of winter winds, particularly in late winter when the air is warm but the soil still frozen, often results in winterkilling of many trees, shrubs, winter wheat, etc. The chief value of protective coverings

Fig. 142.—Limber pine (*Pinus flexilis*) at timber line on Long's Peak, Colorado. Under ordinary conditions this tree grows to a height of 50 feet and has a diameter of 1 to 2 feet. (*Photo by Pool.*)

to tender growing points, such as the scales of buds, is to keep them from drying out. That freezing does them no harm is evident from the appearance of ice crystals on very cold days. The bud scales are cutinized, suberized, or covered with hairs or resin. In addition to furnishing mechanical protection, they also inhibit rapid freezing and thawing, which are most harmful to plants.[585] Because of telescopic expansion, buds may greatly elongate in spring and thus protect the delicate leaves or flowers within (Fig. 143). Hot, dry winds frequently do much damage to vegetation, especially growing crops, by promoting excessive water loss. Wheat and other crops may ripen prematurely and the yield be greatly reduced. At such times, the temperature is high and the humidity very low. Long-continued, warm, dry winds injure blossoms by evaporating the secretion of the stigmas. In the arid Southwest, enormous numbers of cones of evergreen trees die during their first season due to hot, dry winds.

Moist winds exert an opposite influence. Winds that blow across large bodies of water are damp. If constant or frequent, as in certain parts of California, they may permit the growth of mesophytes in an area which would otherwise have a desert vegetation. The distribution of the redwood forests of California is largely controlled by the wind-blown, ocean fogs.[111]

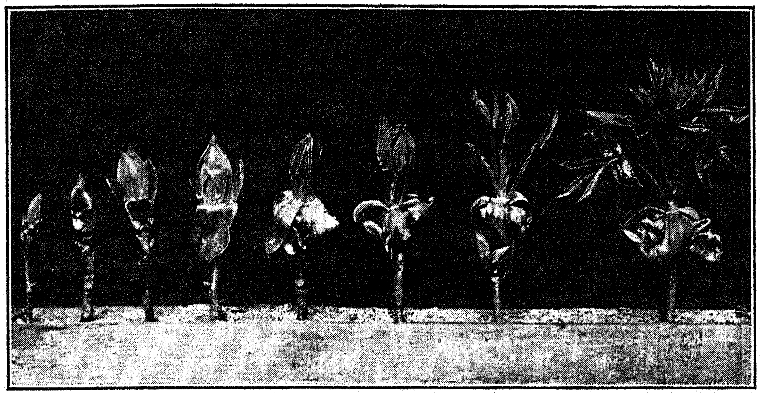

FIG. 143.—Buds of shellbark hickory (*Hicoria ovata*) in different stages of opening. Note the telescopic expansion of the bud scales which finally drop off.

Influence of Pressure and Physiographic Factors.—Pressure influences humidity by varying the density of the air and, hence, its power to hold moisture. At sea level, air with a given temperature will hold more water than air with the same temperature on a mountain top. Fluctuations in pressure are slight and are of little importance except in their relation to rainfall. The effect of humidity is much more pronounced when differences in altitude bring about differences in pressure. One of the most important causes for the dwarfing of alpine plants is increased transpiration resulting from the rarefied air. In addition, these plants have difficulty in rapidly absorbing water from a soil which seldom becomes warm except at the surface.

Exposure, *i.e.* the position of a slope with respect to the sun, affects humidity through the action of sun and wind. Slopes longest exposed to the sun's rays receive the most heat; consequently, slopes with a southern exposure regularly show somewhat lower humidities than those with northern exposures. The effect of wind is most pronounced upon those slopes exposed to prevailingly dry winds. As a rule, these are southern or southwestern, and for reasons of both temperature and wind, these are usually the driest slopes of hills and mountains (Fig. 144).

Cover increases humidity by reducing the influence of both temperature and wind. In addition, a living cover supplies moisture to the air in consequence of transpiration from the plants that compose it. Since

vegetation is giving off water in large amounts, the relative humidity among and just above the plants is greater than that above bare, dry soil. This increase in relative humidity is one of the community effects of vegetation upon the habitat which permits various species to grow because of the decreased transpiration. Differences are often so marked that they have an effect upon the layering of communities as in reed swamps, permitting species to grow near the soil that could not withstand the drier air above.[596] The leaves produced by a single species are, moreover, often more xeric in the upper strata. In fact, this is the case with most tall-growing plants, for example, cereal crops.[290]

FIG. 144.—A sharp ecotone between prairie and forest on a wind-swept slope in eastern Washington. Balsam-root (*Balsamorrhiza*) and xeric grasses are characteristic of the southwest exposures.

To Determine the Effect of the Surrounding Vegetation upon Humidity and Transpiration.—Secure a cylindrical metal container 5 inches in diameter and 11 inches deep that fits loosely into a slightly larger one with perforated bottom. Place the larger container in the center and on a level with the top of a still larger one that should have an area of at least 1 square foot and a depth of 12 inches (Fig. 145). Fill the latter with potting soil compacted to within an inch of the top. Plant thickly seeds of oats, wheat, or brome grass, cover with soil to a suitable depth, and, finally, add a thin mulch of coarse sand or fine gravel. The small, insert container should be filled and seeds planted in a similar manner, after which it should be placed in position in the center of the larger one. Water as necessary but thoroughly the night before the weighings.

On a bright day, when the crop has made a good growth and is at least 6 to 8 inches tall, remove the insert container by the use of two pairs of long-handled pliers and with a minimum of disturbance to the surrounding plants. Weigh it to the nearest half gram and also at the end of each hour throughout the day. During the first hour, place the insert container in a position similar to that which it formerly occupied but away from surrounding plants. During the second hour, place it in the center of

the grass community, thus alternating its position hour by hour. Compare the results with those of another student who left his phytometer in the community the first hour.

Plot the hourly losses and consult the hygrothermograph record for temperature and humidity (p. 265) during the experimental period before drawing your conclusions. What is the paramount factor concerned? How is this affected by the two places of exposure? What other physical factors play a part?

Evaporation from the surface of moist soils increases humidity. This is particularly noticeable in forests and thickets where the air is sheltered from the sun and wind. In general, the air near the soil surface is more moist than that near the top of a cover of vegetation.

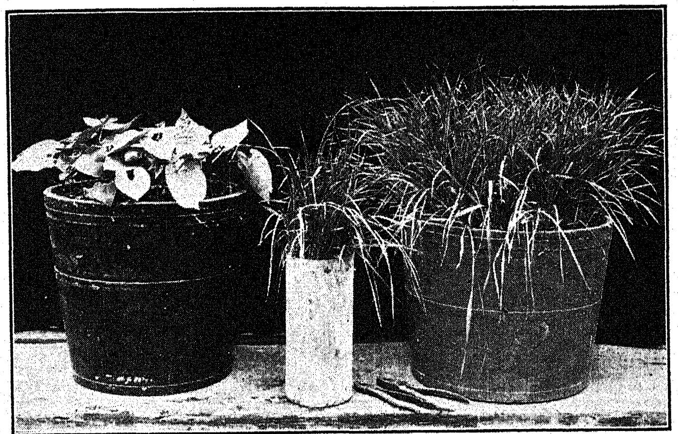

FIG. 145.—Insert phytometers (plant measure) of beans and oats. The latter has been removed from its case in the center of the larger container. The surrounding community has a great influence upon the rate of water loss and photosynthesis. Transpiration is often reduced 30 to over 50 per cent.

Effect of Climate and Habitat.—The general humidity of a habitat depends upon climate and location with respect to bodies of water. Forested regions generally have high humidities, while the humidity of deserts is low. Under the canopy of a tropical rain forest the humidity may remain between 80 and 100 per cent for weeks;[346] in dry grassland or desert it may regularly fall to 15 per cent or less almost every afternoon.[98] Coastal regions are moist, provided the wind does not blow continuously offshore; inland regions are relatively dry; lowlands are more humid; and tablelands and mountains usually less humid.

In a particular habitat the relative humidity approaches or reaches saturation during a rain or fog and then often gradually diminishes to a minimum just before the next rainstorm. There is also a daily maximum and minimum. The highest relative humidity, except when disturbed by cloudy or rainy weather, usually occurs near the time of sunrise, and the minimum from 2 to 4 hours after noon, or the reverse of the hours of the

occurrence of the maximum and minimum temperatures. Variations within the habitat chiefly arise through differences in protection from sun and wind.

Measurement of Humidity.—Humidity is measured by means of a psychrometer (chill measure). There are three types of psychrometers, the sling, cog, and stationary (Fig. 146). All consist of a wet-bulb and a dry-bulb thermometer set in a case. The dry-bulb thermometer is an ordinary thermometer, but the wet-bulb is one covered with a clean linen cloth which is moistened with distilled water. In using the sling or cog psychrometer, the thermometers are whirled about in the air. The dry-bulb thermometer indicates the normal temperature of the air, the wet-bulb instrument gives the reduced temperature resulting from chilling due to evaporation.

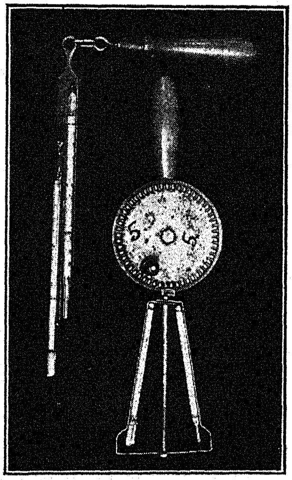

FIG. 146.—Sling and cog psychrometers. The latter is about 14 inches long.

If the air is moist, there is little evaporation; if it is dry, evaporation is rapid and the result is a marked "depression of the wet bulb." Evaporation produces a decrease in temperature depending upon the amount of moisture in the air. Tables have been prepared for almost all possible combinations of air temperatures and wet-bulb depressions, showing the corresponding relative humidities.

For field work, the cog psychrometer is the most convenient and satisfactory. Since the instrument must be moved about in order to prevent the accumulation of moisture about the wet bulb, the stationary psychrometer is of little value. The sling psychrometer is liable to be broken in using unless there is a space free from vegetation for a distance of 2 yards. The cog psychrometer is smaller, more compact, and the danger of breaking in use or in carriage is extremely small. It has the further advantage of making it possible to take readings among plants and in layers of air only a few centimeters in thickness and in any position.[191] To secure the necessary temperature range, centigrade thermometers are used and the readings thus obtained converted into Fahrenheit temperatures (by multiplying by 1.8 and adding 32) before the humidity can be determined from the tables.

Making a Reading.—Considerable practice is needed in making an accurate reading. In general, observations should be taken facing the wind and preferably in the shade of the body, although they may be made in full sunshine with but slight error. It is also a wise precaution to shift the position of the instrument a foot or more during the reading, except when the humidity of a definite layer is desired. The cloth of the wet

bulb is first moistened with clean water. Distilled water is preferable but tap water and the water from streams may be used without appreciable error if the cloth about the wet bulb is changed occasionally to prevent the accumulation of dissolved material. The water is poured slowly upon the cloth of the bulb until it is completely saturated, the excess shaken off, and care taken not to wet the dry bulb. As the cloth slowly absorbs water when perfectly dry, a pipette or a brush is usually a valuable aid in quickly wetting it.

The temperature of the water is of slight consequence, though readings can be made more quickly when the temperature is not too far from that of the air. The psychrometer is held so that the bulbs are in the layer of air to be studied and rotated at an even, moderate rate. As the reading must be made when the mercury of the wet bulb reaches the lowest point, the instrument is usually stopped after 100 revolutions, and the position of the column is noted. The lowest point is often indicated by the tendency of the mercury to remain stationary. As a rule, the lowest point can be known with certainty only when the next glance shows a rise in the column. Check readings of this nature must be made at the end of every 25 or 50 revolutions in order to make sure that the mercury has not reached the minimum and then begun to rise while the instrument is in motion. In noting the final reading, care must be taken to secure it before the mercury begins to rise in consequence of stopping the movement. For this reason, it is desirable to shade the psychrometer with the body when looking at it in the sunshine and to take pains not to breathe upon the bulbs or to bring them too near the body. At the moment when the wet bulb registers the lowest point, the dry bulb should also be read and the results recorded.

Use of Humidity Tables.—To ascertain the humidity, the difference between the wet- and dry-bulb readings is obtained. This difference together with the dry-bulb temperature (in degrees Fahrenheit) is referred to the tables. A variation in temperature has less effect than a variation in difference. In consequence, the dry-bulb reading is expressed in the nearest unit, and the difference is reckoned to the nearest half degree. Since the humidity varies with the air pressure, it is necessary to use the table computed for the normal barometric pressure of the place under consideration. Humidity tables are usually computed for pressures of 30, 29, 27, 25, and 23 inches. For mountainous regions over 7,000 feet high, additional tables are desirable, but the table of 23 inches will meet all ordinary requirements, since the effect of pressure is small within the usual range of growing-period temperatures.

The Hygrograph.—A continuous record of humidity may be obtained by means of the hygrograph. This consists essentially of strands of human hair about 8 inches long, clamped at both ends. In moist air the hairs become longer, in dry air, shorter. They are attached to a

lever in such a manner that a pen which writes on a rotary drum is raised with an increase in humidity and lowered in dry air.

Experience has shown that the hygrograph gives fairly reliable humidity records in dry climates but must be frequently checked in moist ones where it is exposed to high humidities. This is done by means of a cog psychrometer, and the pen is then adjusted on the drum to show the proper percentage of humidity. The initial adjustment, of course, is made in the same way, the hairs being stretched tighter or loosened by turning the screw supporting the frame upon which they are held.

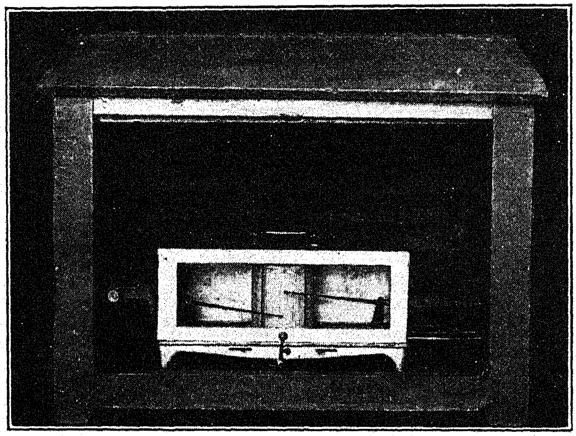

FIG. 147.—Hygrothermograph and shelter. The hairs regulating the humidity pen are on the left under the protecting shelf; the silvered thermometric bar regulating the temperature pen is on the right. The door of the shelter has been removed.

It is convenient for comparison to record both humidity and air temperature upon the same record sheet. The temperature pen is regulated by means of the expansion and contraction of a silvered thermometric bar exposed to the air. Such an instrument is called a *hygrothermograph* (Fig. 147). The temperature records are thoroughly reliable and the instrument need be checked only once or twice a week. At the end of the week the clock is wound, a new record sheet placed on the drum, and the pens inked. The humidity pen should be filled with the green ink, the one recording temperature with the purple ink. Upon removal of the record, the station and date are recorded. Care should be exercised to see that the pens are set on the line indicating the proper time of day and that they do not interfere in passing each other near the middle of the record sheet. It is best to adjust the instrument at a time when the humidity is not changing too rapidly, *i.e.* between 10 a.m. and 4 p.m. The pens must be released at the end of the week or they will buckle against the vertical bar which holds the record on the drum.

The hygrothermograph should be properly housed in a well ventilated, waterproof, wooden shelter painted a light green. This should be lined

with a small-meshed wire screen to prevent the entrance of large insects and furnished with a removable door. The shelter should be of sufficient size to permit the opening of the instrument without its removal and to store the necessary equipment for adjusting the recording devices, *viz.* psychrometer, small bottle of distilled water, humidity table, camel's-hair brush for dusting the hairs, glycerin inks, and a standardized Fahrenheit thermometer. The shelter, with the floor level, should be fastened firmly in place by means of strong stakes. The door should open to the north, so that the sun can not shine upon the instrument, and be furnished with a good lock.

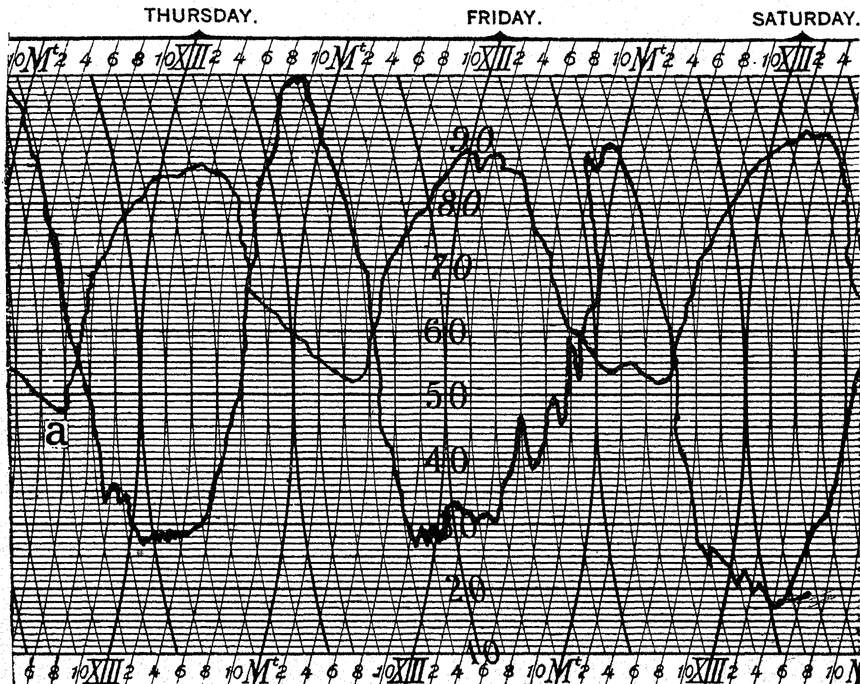

FIG. 148.—Portion of a hygrothermograph record showing the temperature (line *a*) and humidity in the short-grass plains from June 30 to July 2, 1921. At what time was the maximum air temperature reached? Does the lowest humidity occur at about the same time? Why?

Interpreting the Records.—It should be observed that the hygrothermograph records are ruled in two arcs corresponding with those described by the temperature and humidity pens, respectively. The time of day for the temperature pen (XII indicating noon and M midnight) in 2-hour intervals is indicated at the top of the record sheet, that for humidity at the bottom. The numbers on the horizontal lines ranging from 10 to 100 indicate both percentage of humidity and degrees Fahrenheit. Thus, in Fig. 148, the humidity at 4 p.m., June 30, was 28 per cent and the tempera-

ture 85°F. The next morning at 4 a.m. when the temperature had fallen to 53°, the humidity was 100 per cent.

Constructing Graphs.—Where it is desired to obtain the average daily humidity (or temperature) by weeks, this may be done as follows: Add the humidity at the 2-hour intervals for the entire week and divide by the total number of intervals. If it is desired to ascertain the average day humidity, which is of most importance to vegetation, add all of the 2-hour readings beginning at 6 or 8 a.m. (according to the season) to 6 p.m. inclusive, continuing for the 7 days, and divide by the total number of readings. From these data, graphs similar to those in Fig. 152 may be constructed, and the humidity (or temperature) of different communities compared.

Periods of low relative humidity are very trying for vegetation, since they almost invariably occur at times when water content is also low. The weekly record should be given careful study since such periods are usually more important than the averages. During times of protracted low water content and low humidities, some types of vegetation remain dormant.

To Measure Relative Humidity.—With the cooperation of two or more other students, make simultaneous readings every half hour of the relative humidity in several adjacent stations such as thicket, woodland, prairie, or swamp. Plot the results in the form of graphs. Also, make readings at the same station at different levels. Operate a hygrothermograph on a lawn, in a grove, or in other vegetation where the instrument may be observed and frequently checked. If possible, secure two instruments and compare the humidity and temperature in two different habitats.

WIND

The effect of wind in modifying humidity has been discussed; its mechanical and erosive effects will now be considered.[161] Because of the friction of the soil surface and masses of vegetation, the velocity and, hence, the pressure exerted by the wind rapidly increases with height. This explains the greater velocity attained on exposed seacoasts and at higher altitudes that are free from or above the obstructions created by masses of vegetation. By its strength, wind may destroy large areas of timber and do much damage by blowing down crops. Often, only branches or twigs are broken or leaves (*e.g.* wheat, corn, etc.) torn by wind whipping. The actual pressure exerted by the wind depends upon the character and dimensions of the surface as well as the density of the air. At sea level, a wind with a velocity of 10 miles per hour exerts a pressure of approximately ⅓ pound per square foot; at 30 miles, this is increased to about 2.5 pounds; but over 9 pounds pressure per square foot is exerted at a velocity of 60 miles.[498] Even higher velocities and pressures occur, especially on mountain tops.[165] By its persistence, it causes permanent curvatures and malformations of plants upon which it impinges.

Wind-driven dust, snow, and hail exercise a marked abrasive effect upon vegetation, sometimes to the extent of wearing away the bark of trees or shrubs in wind-swept areas. The blowing of soil is an ever present menace during the spring months in the Great Plains and many other regions. The surface of whole fields is blown away and the soil deposited on others. In both the process of erosion and of deposit, the crop may be destroyed.[82] Even clay soil may be loosened and transported. In muck land damage is often great, the light, organic materials being readily removed unless the soil is kept damp or protected from the wind.[214] Blowing of soil reaches its maximum in sand where destructive "blow-outs" occur, and valuable forests, etc., are sometimes covered by dunes.[441]

The wind may do much harm in blowing fruits or blossoms from trees or other plants and by preventing insects from working among the flowers. It is an important agent in the distribution of weeds and spores of many disease-producing fungi, such as rusts, chestnut blight, etc. By means of whirlwinds, heat waves, and convection currents, spores are carried high into the air and over long distances. Viable spores have been caught at heights of more than 11,000 feet.[510] Conversely, the wind has a beneficial effect in drying the soil in spring and in equalizing temperature on the leeward sides of large bodies of water. By mixing the cold and warm air, wind sometimes prevents frost damage on cold, clear nights. The warm, dry, chinook winds of mountainous regions, particularly marked in Montana and Wyoming, cause the snow to evaporate very rapidly and leave the ranges available for winter grazing.

Modifying Wind Movement.—The force of the wind may be modified in a number of ways, *viz.* by windbreaks, by sowing grain in furrows, and, on sandy land, by "strip planting," etc. Strip planting consists of growing various crops, *e.g.* corn, wheat, sorghum, or native hay, in alternate, long, narrow strips at right angles to the prevailing wind. This reduces the wind effect, since at all times a part of the soil in the field is protected by a cover of vegetation.[461] In dry lands the method of seeding the grain in furrows somewhat deeper and farther apart than those made by the ordinary wheat drill has many advantages. Not only does it promote better and more certain germination when the surface soil is dry, but the furrows also retain the snow, which otherwise might be blown from the field, and give better protection to the grain during times of low temperatures and high winds. There is, moreover, less injury from the heaving of the soil as a result of alternate thawing and freezing in spring and less injury from soil blowing and from drought.[429]

Windbreaks usually consist of a row or rows of trees or shrubs, groves, etc., planted on the side of the field so as to break the force of the prevailing wind. The influence of windbreaks on wind velocity varies with their height and density and much depends also upon the topography.

The general effect is to reduce transpiration. Soil moisture is conserved and evaporation frequently reduced 30 to 65 per cent. Windbreaks check the movement of the surface soil, prevent the drifting of snow on the leeward side, greatly reduce the lodging of grain and the falling of fruit, and increase the day temperature. On the north side of a windbreak for a distance varying from one-half to its total height, the growth of crops is reduced due to shading. The decrease in normal yield is often extended further by the reduction of water content due to absorption by the roots of the trees (Fig. 149). In the protected area beyond, to a distance of four to ten times the height of the windbreak, yields are increased. For example, the yield of wheat has been increased 10

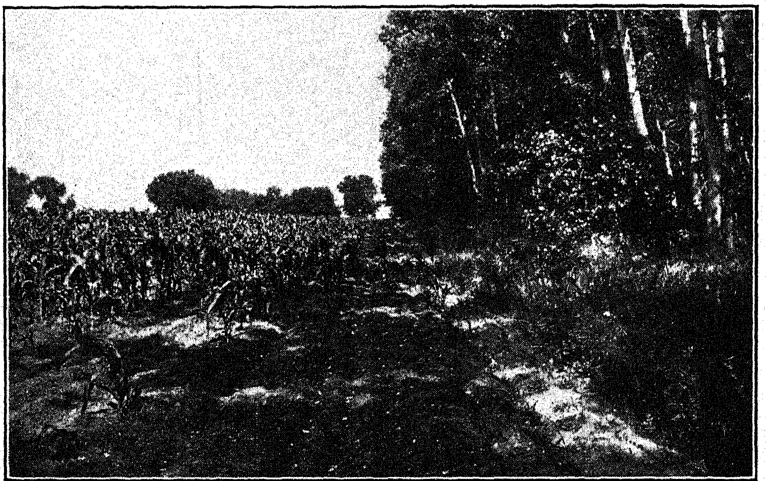

Fig. 149.—A cottonwood grove forming a windbreak. Corn within a few rods north of the windbreak is badly damaged by shade and reduced water content. (*After Bates.*)

bushels per acre and that of corn 18 bushels, where the protection was most complete, over that in unprotected parts of the field. Thus, the total effect is an increased yield. The windbreaks are profitable, moreover, because of their high value for timber and fuel.[20]

The way in which man may modify the local environment, even of a desert, is well illustrated in certain irrigated orchards in California, which have been planted to alfalfa and shielded by an efficient windbreak. Factor measurements made in such orchards and in the desert to windward show that the climatic complex is greatly ameliorated. The alfalfa transpires at a tremendous rate and literally bathes the trees in a moist atmosphere. The windbreak retards the movement of the relatively moist air away from the vicinity. The evaporation of the water from the soil and plants tends to lower the temperature of the air. As the soil is largely shaded, the high soil temperatures are also reduced.[104]

Measuring Wind Velocity.—Wind velocity is measured by a rotating anemometer (wind measure), as shown in Fig. 150. The standard Weather-Bureau anemometer is the most practical for field work, although the simple form of hand anemometer is useful in ascertaining the effects of cover. The latter records wind movement in feet per minute. The standard anemometer is practically a self-recording instrument, the wind velocity being registered up to 1,000 miles, but as the dials run on without any indication of the total number of revolutions, it should be visited and read each day. Directions for reading the dials (to 0.1 mile) accompany the instrument.

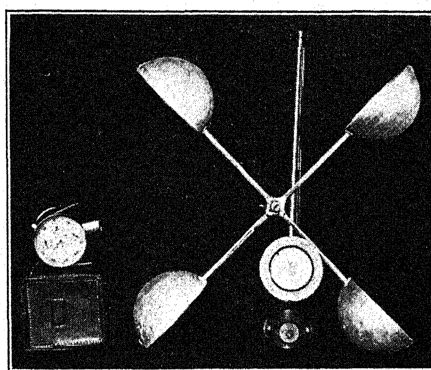

FIG. 150.—Two types of anemometers. The cups of the Weather-Bureau type on the right have been detached from the top of the stem by means of loosening the setscrew. Hand anemometer on the left.

The anemometer is securely fastened by means of a thumbscrew to a stake driven vertically into the ground. Readings are ordinarily taken with the revolving cups at the general level of the vegetation. Care should be exercised that their movement is not retarded by contact with the growing plants. In some cases, it is necessary to dig a pit for the stem of the anemometer in order that the cups may be at the same height as that of low-growing vegetation. For comparative readings, two or more instruments should be operated at different heights and long-time readings of wind movement obtained from different plant communities. The data are recorded as miles of wind movement per hour.

To Measure Wind Velocity.—Secure two anemometers of the weather-bureau type. Operate them at different levels in various plant communities during a period of 1 or more days (*e.g.* in prairie just at the height of the vegetation and 3 feet above). Also, compare the wind movement at the same level in different plant communities. By means of hand anemometers make simultaneous readings of wind movement in a field of grain, clover, meadow, etc., below the level of the vegetation and just above it.

EVAPORATION

A knowledge of the humidity, wind movement, air temperature, and sunshine of a habitat throws much light upon the environment in which plants grow and vegetation develops. The desiccating power or "evaporation stress" of the atmosphere as affected by all of these factors is of great importance to plants. Much emphasis has been laid upon the water content of soil as directly determining the character of vegetation and its rate of development. Of almost equal importance is the loss

through transpiration of moisture that is absorbed. The evaporation rate, when measured directly, gives the integrated effect of humidity, radiant energy (*i.e.* temperature and light), and wind. While there is no instrument that integrates the effect of these different stimuli to water loss in a manner similar to that of plants, yet this objective has been attained to some extent. Indeed, different plants, because of differences in stomatal movement, density of cell sap, colloidal content of cells, incipient drying, etc., respond differently. Nevertheless, the process of evaporation from a suitable evaporating surface (*e.g.* porous clay cup) is closely similar to that from a plant body. The readings of the loss of water from atmometers (vapor measure) placed at the general level of the transpiring vegetation in different habitats give one of the most useful records of the evaporation stress of the air as it affects the surrounding vegetation.

Measurement of Evaporation.—Evaporation is measured in a number of ways. At many state and federal experiment stations the rate of water loss in inches is determined for the 6 summer months (April to September) from large open tanks.[51] These circular tanks of galvanized iron are 8 feet in diameter and 2 feet deep. They are set 20 inches deep in the soil and filled with water to within 4 inches of the top. The amount of water evaporated is determined by means of a gage, corrections being made for precipitation during the interval between readings. The rate of evaporation from water in a tank is about the same as from a wet soil surface, although it is greater from the latter where the soil is dark in color. Many valuable data have thus been obtained for broad climatological studies, but obviously such a method is quite impracticable for measuring evaporation in different plant communities.

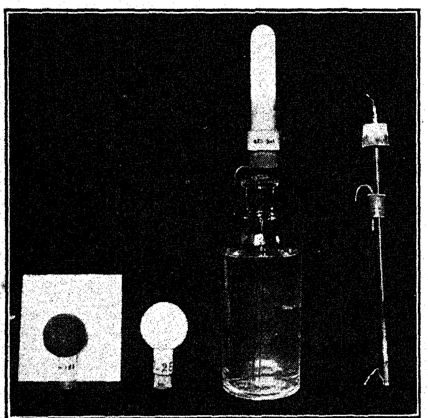

Fig. 151.—Porous cup atmometers. The non-absorbing device with wool plugs and mercury trap is shown on the right.

The evaporimeters most widely used are the porous, clay-cup atmometers devised by Livingston.[314] These are either cylindrical or spherical in shape and white or black in color (Fig. 151). The cups are made of a very fine grade of clay. The lower part is waterproofed with varnish or shellac and the evaporating surface thus reduced to a definite area. The porous surface should never be handled, since the pores will become clogged with oil or dirt.

In operating, the cup is first filled with distilled water and allowed to stand for a short time until the clay walls have become saturated. It is then again filled and stoppered tightly with a rubber cork through which a glass tube extends. The excess water is forced into the tube. The apparatus is quickly inverted and the second cork on the tube (which must be full of water) inserted into the supply bottle, air bubbles being excluded. The latter should contain about a quart of distilled water. As the water evaporates from the outer surface of the cup, it is supplied by the rise of fresh water from the bottle, so that the cup is always full. A curved tube through the bottle stopper, drawn to a capillary point, permits the equalization of the air pressure without permitting the exit or entry of water. The bottle is filled to a file scratch on the neck, and the loss of water is determined by the number of cubic centimeters used in refilling it.

Spherical cups have the advantage of always exposing half of their surface directly to the sun regardless of its altitude. The black cups absorb more radiant energy than the white ones and consequently give higher evaporation losses during the day. In fact, the differences in the losses from the white and black cups exposed in the same place have been used as a measure of radiant energy (light).[66] The losses from one kind of cup or other evaporating system can not be directly compared with those from another. Perhaps it is for this reason that the white cylindrical cups which were the first to be made are still widely employed.

Obviously, if the atmometer cup permits of evaporation, it will also absorb water during rain. To prevent its doing the latter, numerous non-absorbing devices have been made (Fig. 151). These consist of mercury traps so arranged that while water may be drawn into the cup, its movement in the reverse direction is prohibited.[529] Non-absorbing mountings, although absolutely necessary for reliable field readings, somewhat complicate the apparatus. In the simplest form, a twisted wool plug is inserted into one end of the tube, about a centimeter of mercury placed above it, and a second plug put in place at the opposite end. Water is sucked into the tube and the plugs well soaked. The rubber stopper, through which the tube extends, is then forced into the inverted, water-filled atmometer in the usual manner.

Owing to the variations in the clay in the cups, different atmometers give different evaporation losses per unit of surface. But every cup is standardized by comparison with a standard cup whose rate of evaporation under certain uniform conditions is known. Each cup bears a number and a coefficient. By multiplying the actual loss from the cup during a given period by its coefficient, the loss from the standard cup, had it been used, is obtained. For example, cup 947, coefficient 0.70, evaporated 140 cubic centimeters. The corrected loss is 98 cubic centi-

meters. Thus, evaporation rates from widely different habitats or countries may be directly compared.[171,558]

To prevent the pores of the cup from becoming filled with impurities, especially lime, only distilled water should be used. Rinsing occasionally with weak corrosive sublimate prevents the growth of algæ, bacteria, and fungi. The cups may also be cleaned from time to time with a stiff toothbrush and distilled water. If these precautions are taken, the rate of water loss from the cup under identical conditions varies but little. After a few weeks use, however, they should be restandardized.

Making Readings.—For hourly readings or those for shorter intervals, the cups should be mounted on small graduates, corrections being made for the space occupied by the glass tube.[446] In field practice, readings are made daily or weekly. Evaporation rates are measured for the purpose of determining how great an evaporation stress the plant or vegetation has to withstand and can withstand without injury. Critical periods are sometimes brought about by high evaporation stress when water content is abundant, but usually they occur and are most harmful when it is very low. Careful attention should be given evaporation during such periods; they may be obscured in the average weekly record. Evaporation records are of less significance, moreover, at a time when vegetation is dormant, whether as a result of drought or of cold. For example, evaporation losses are usually highest on the short-grass plains at a time when the dominant grasses (*Bulbilis*, *Bouteloua*, etc.) have dried and cured on the ground.

Position in the Field.—The exact position of the atmometer in the field is determined by the object in view. If this is to ascertain the evaporation losses about seedlings on the forest floor, the cups should be placed at the same height as the transpiring seedlings. Fully grown undershrubs are transpiring at a different level, and the tops of the crowns of trees are subject to a much greater evaporation stress.[170] In swamps, for example, the evaporation rate rapidly increases with height. It may vary from 100 per cent at the level of the highest vegetation to 30 per cent at half this height and fall to only 7 per cent near the wet soil surface. Thus, evaporation gives a direct clue to layering of vegetation.[184,596]

Many plants as well as soft-bodied insects are confined to the lower layer, although the latter frequently move to higher levels at night or on cloudy days when the evaporation stress is decreased. Consequently, the atmometer should be placed at the level where the evaporation rate is to be determined. In grassland, it is the rule to place the cups at the general level of the mass of vegetation, none of which is allowed to touch the cups. Usually, it is necessary to excavate a hole in the soil to receive the bottle. This should be done with a minimum of disturbance to the vegetation, and to prevent caving, it should be lined with a cylinder of light, galvanized iron sunk flush with the soil.

Comparison of Data.—Readings at the several stations should be made as nearly at the same time of day as practicable and in the same sequence. The corrected readings from the various habitats or partial habitats may then be directly compared. If they are taken at regular intervals over a considerable period of time, comparison is best made by means of a series of graphs, as shown in Fig. 152.

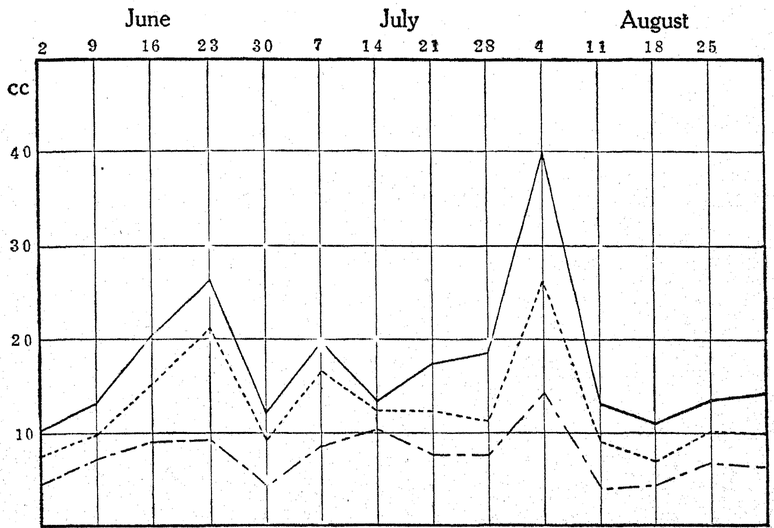

FIG. 152.—Graphs showing the average daily evaporation by weeks in prairie (upper line), hazelnut thicket (middle), and linden forest, in southeastern Nebraska during 1917.

To Measure Evaporation.—Equip atmometers with non-absorbing devices and measure the evaporation losses at the same level in two or more plant communities. Also, compare the relative rates of evaporation in the same community, and preferably in one that shows well-marked layers, at different heights above the soil surface. What is the order of importance of the several factors that influence evaporation? Give reasons for this.

Evaporation and Plant Distribution.—The rate of evaporation has a marked influence not only on the amount of the water lost from plants through transpiration but also in reducing the water content of the soil. The latter is an important feature, especially in dry regions. Evaporation determines the efficiency of rainfall in a great measure, especially where the rainfall is less than 30 inches annually.

In Montana, where evaporation is low, 14 inches of precipitation is sufficient to support a good growth of short grasses; 17 inches are required in Colorado; and 21 inches in Texas. Evaporation from the large, open tank in Montana during the 6 summer months is 33 inches, but it is 54 inches in northwestern Texas. The extra 7 inches of precipitation are needed to counteract the higher evaporation rate in Texas. Similarly,

the rate of evaporation increases from about 30 inches in North Dakota to 60 inches in southwestern Kansas. Since it requires nearly 10 inches of rainfall to offset the extra 30 inches of evaporation, it is apparent why under 20 inches of rainfall in North Dakota tall-grass prairie is well developed and excellent crops of spring wheat are grown, while under a similar rainfall in western Kansas short-grass vegetation thrives and only the most drought-enduring crops such as Kafir and milo are cultivated. Thus, the lines of equivalent rainfall, because of the factor of evaporation, extend much farther eastward than do those of actual rainfall.[51]

The effect of the rate of evaporation upon transpiration alone is marked. It requires only 518 tons of water to produce a ton of alfalfa near the Canadian line at Williston, N. D.; 853 tons at Akron in eastern Colorado; but 1,005 tons are required at Dalhart in the Panhandle of Texas.[55] During the years 1911 and 1913, the average water requirement (*i.e.* the pounds of water used to produce a pound of dry matter) of 25 varieties of crops grown at Akron, Colo., was approximately 21 per cent greater than during 1912. This was due almost entirely to a decrease of 25 per cent in the evaporation rate in 1912, resulting from decreased solar radiation caused by fine volcanic dust in the upper air from Mt. Katmai, Alaska.[53]

The ratio of precipitation to evaporation gives the nearest approach that is yet possible toward an ideal index of the external moisture relations of plants. The rainfall-evaporation ratio at Lincoln, Nebr., is approximately 60 per cent. The line with this ratio extends northwestward across the Dakotas and nearly straight southward into Texas. In general, the drier types of grassland lie between lines with ratios of 60 and 20 per cent. The desert has a lower ratio. Between 60 and 80 to 85 per cent, tall-grass prairie abounds; eastward where the ratio is greater than 100, *i.e.* where rainfall exceeds evaporation, continuous forests occur.[541] Unfortunately, evaporation data over North America as a whole are very meager, and the preceding data apply only to the conditions during a single year. Were evaporation data available in quantity similar to that of precipitation, a much clearer picture of the water relations in connection with plant distribution would be possible.

CHAPTER XII

TEMPERATURE

Temperature is like water in its action upon plants in that it has more or less to do with nearly every function, but as a working condition and not as a material. All the chemical processes of metabolism and also many physical processes such as diffusion, precipitation, and coagulation as in cell-wall formation, etc., are dependent upon temperature and accelerated by its increase up to an optimum. With a decrease in temperature to a certain minimum, growth in size is retarded; at lower temperatures, cell division and photosynthesis are also checked; and, at a still lower minimum, respiration ceases and death ensues. Thus, temperature is not only necessary for life processes but also furnishes the energy for some of them. Radiant energy, for example, is absorbed in photosynthesis and set free in respiration.

The responses to the stimulus of temperature are not localized in a particular organ but occur everywhere in the protoplasm throughout the living tissues. Temperature has no direct formative effect on the structure of the plant, except in so far as it affects the rate of growth. It does, however, have a profound influence in altering not only the rate but also the products of metabolism. At low temperatures, for example, many plants elaborate an abundance of polysaccharides.

The habitat plays an important part in determining the influence of temperature upon each species. A particular species has been accustomed for countless generations to certain extremes of heat and cold as well as to certain seasonal sums of temperature. Temperatures beyond these extremes check the plant's activity and this is usually true of the total heat available during the growing period. These temperature adjustments become so deeply impressed in the protoplasm of a species that there results a more or less fixed habit as regards temperature. Thus, in temperate regions, for example in deciduous forests, low temperatures of winter become a necessary experience to the trees. It is a phase of the environment to be endured and, also, a necessary means of stimulating developmental vigor. Winter is not a recurrent catastrophe to vegetation but a stimulus to renewed growth. The effect of habitat is well shown by many seeds, bulbs, corms, tubers, buds, etc., which are merely plantlets or growing points securely protected against drought. They have accommodated themselves to a long period of cold, in consequence of which it is often impossible to cause them to grow

without either naturally or artificially subjecting them to cold[121,140,141] (Fig. 153).

In connection with germination, temperature has a marked influence upon ecesis; it greatly modifies growth; and in the opening and closing of flowers and flower heads it has a direct effect upon reproduction.[459] Consequently, it not only has an effect upon the individual but also upon the development of vegetation as well.

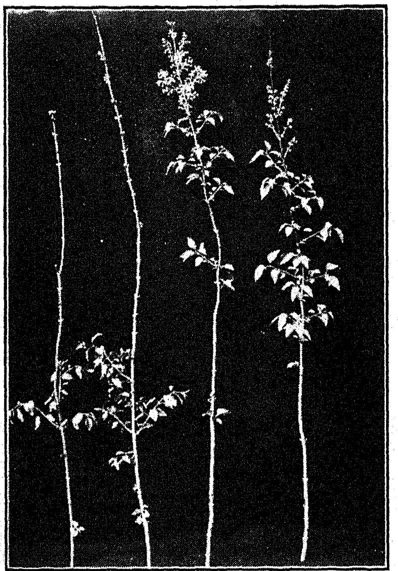

FIG. 153.—Two branches from a Persian lilac (left) that wintered out of doors except the ends of the branches which were admitted through an opening into a greenhouse. On the right are two branches from a lilac wintering in a greenhouse, except the ends of the branches which extended outside. Photograph made on March 1, 3 weeks after all parts of both plants were placed in the greenhouse. Note that only rarely has a bud opened except on the parts of the stems that have been chilled.

Measurement of Temperature.—With the aid of a thermometer, the measurement of temperature is an easy task. In determining the temperature of the air, direct or reflected sunlight must be excluded from the thermometer as fully as possible. The thermometers should be standardized instruments, reading accurately at least to 1 degree, since the errors in cheap thermometers are not uncommonly as great as the differences between two conditions that are being studied. As these are both delicate and expensive, they must be used with great care, particularly in the field. To prevent breakage, they should be carried in felt-lined, individual brass cases. In making readings of air temperature, precautions are necessary to expose the bulb to the full effect of the wind, if any, and to keep it away from the hand or body. The instrument must be left in position until the mercury becomes stationary. In some cases, as when the wind blows fitfully, the mercury constantly rises and falls. The mean of the fluctuation is taken as the proper reading. Temperature readings in the surface of the soil are made with the bulb just covered with soil; these should be supplemented by a reading on the surface.

Since temperature is an extremely variable factor, isolated readings are of little value, and it is best to use automatic thermometers or thermographs. Maximum and minimum thermometers may be used to record the extreme temperatures during day and night.[539] The maximum is a mercurial thermometer with a constriction in the tube just

above the bulb; this allows the mercury to pass out as it expands but prevents it from running back, thus registering the maximum temperature. The minimum thermometer contains alcohol. The column carries a tiny dumb-bell-shaped marker which moves down with it but will not rise as the liquid expands. This is due to the fact that the liquid expands too slowly to carry the marker upward, while the surface tension causes it to be drawn downward as the fluid contracts. The thermometers are mounted in an oblique position. The mercury of the maximum thermometer is driven back into the bulb by rapid whirling and the thermometer then placed with the bulb slightly elevated. The minimum thermometer is set for registering by raising the free (lower) end so that the marker runs to the end of the column and is then placed in a level position.

These thermometers should be exposed in an appropriate shelter which must not absorb radiant energy sufficiently to become heated within. This danger is largely overcome by the use of a double roof, a partly open floor, and walls made of slats which sufficiently overlap to exclude overhead light but not enough to retard the free circulation of air.

To Determine Maximum and Minimum Temperatures.—Place properly sheltered maximum and minimum thermometers in each of two communities, preferably in early spring or late fall. Obtain and compare the highest and lowest temperatures during a period of several days. Also, determine the minimum temperatures in valleys or depressions and on adjacent hilltops or bench lands (p. 285). Explain the differences obtained in the two sites.

Obviously, the most valuable record of temperature is a continuous one, such as is obtained by means of a thermograph. This should be set up and appropriately housed in the field, preferably two or more being simultaneously operated in different habitats. For a comprehensive study of a layered plant community, such as a forest, more than one will be required, for temperatures and temperature variations of different layers may be widely different. A study of the thermograph records will reveal many things not shown by the maximum and minimum readings. It will show not only when the high and low temperatures occur but also how long they persist. The time relation is an extremely important one. In open thickets or woodland, for example, the sun may shine directly upon the shade plants and so reduce the humidity and promote transpiration as to cause them to droop. Because of little air movement, a high temperature is attained. But soon the plants are again in the shade and absorption overtakes water loss. Were the high temperatures and consequently decreased humidity maintained, these mesophytes might succumb.

The greater number of species and of individuals pass through their entire life cycle without being exposed to extreme heat or cold. Extremes

of temperature have little significance for them. Low-temperature effects are confined to plants that appear very early in the growing period and those that linger toward the close. Notwithstanding the fundamental relation of temperature to plant metabolism and its general controlling influence on growth, in developmental communities at least, the measurement of temperatures is not of primary importance. The water content of soil, humidity, and light are usually the decisive factors in determining the relation of a community to neighboring ones. Each community usually exists well within the temperature limits that might be critical for it, and the indirect effect of temperature on humidity and evaporation is nearly always of greatest importance.

Temperature Records.—Mean annual temperatures are of practically no value in a study of vegetation, because they take no account of season. The mean annual temperature in certain parts of Siberia is −15°C. This is very much below the minimum at which any vegetation could grow, yet here is a forested region. The summer is short but hot. Not only are the forest trees able to grow and mature seed but also a luxuriant herbaceous vegetation abounds.

Monthly means are much more significant in conveying an idea of the temperature relations, and the monthly-mean maxima and minima are the most useful temperature data published by meteorological stations. Maximum and minimum temperatures are very important factors in the development of vegetation, since plants and particularly cultivated crops may be damaged by a few hours of excessive heat or killed by a brief period of low (usually freezing) temperatures. Weekly means are more valuable than monthly means in studying the relation between temperature and plant growth. Most valuable of all, however, are the daily temperature records. This is true particularly of the occurrence and endurance of high or low temperatures during the early and late portions of the growing season, as well as at times of extremes throughout the whole growing period. Together with a record of humidity, they are of the highest value in the study of environment. They can be had only by securing a continuous record during the successive days by means of a hygrothermograph.

The mean temperature for the day is approximated, where minimum and maximum thermometers only are used, by averaging the two readings. Where a thermograph is employed, a nearer approach to the true mean may be obtained from the sum of the hourly temperatures divided by 24. It is sufficiently accurate to average the readings of the even hours. The average day and night temperatures for weekly periods may also be determined. These may be plotted in the usual way for comparing the temperatures in different habitats or in different strata of the same habitat. The daily maximum and daily minimum for weekly periods may be similarly compared. Mean maximum and mean mini-

mum temperatures are often more important to vegetation than the mean daily temperatures because they represent more clearly the actual range of temperatures that plants experience.

Plant Temperatures.—The temperature of the plant tends to follow closely that of its environment.[319] Unlike warm-blooded animals, plants do not possess temperatures that are independent of the surrounding medium. In general, stems or leaves are never very much warmer or cooler than the air that surrounds them and roots can seldom possess a temperature very different from that of the soil. Certain plant activities, notably respiration, bring about an evolution of heat. But since respiration is vigorous only at relatively high temperatures and the rate decreases with a lowering of temperature; the amount of heat produced is little when an increase in temperature may be most needed. Even, when vital processes are most vigorous, a marked rise in temperature is prevented by outward conduction and radiation. Similarly, any considerable decrease in the temperature of the tissue is automatically adjusted by intake of heat from without.[27]

There are exceptions to the rule, however, that are worthy of mention. The temperature of the plant, especially that of stems and leaves, is not always that of the surrounding medium. In case of a sudden change in temperature, the plant responds more slowly than the air, and its temperature is for a time higher or lower. This is due to the abundance of water and its high specific heat. The plant lags in the change in proportion to its mass and surface. This is well illustrated in certain cacti where they are unharmed by a few hours of freezing temperatures but are killed by a longer exposure, for example, 19 hours in the giant cactus (*Carnegiea gigantea*).[477]

In winter, under direct sunshine, differences as great as 25°C. occur on the south and north sides of tree trunks just beneath the bark. Every cloud obscuring the sun for a few minutes will cause the bark to freeze if the air temperature is sufficiently low. With the passing of the cloud the cambium may warm up above its freezing point within a few minutes. Changes of 10°C. sometimes occur within a period of 3 minutes. The high temperature, accompanied by rapid evaporation during the day, falls rapidly after sunset. The pronounced change may cause the death of the tissue next to the wood and the subsequent peeling of the bark. These internal temperature fluctuations are important on account of their relation to sun scald, crotch injury, frost cracks, etc., found among trees of northern climates. They result in openings that afford entrance to wood-rotting fungi. In spring, the higher temperatures of the sunny side may result in a decrease in hardiness of the tissue exposed to the sun, with a break in dormancy and attendant injury upon sudden freezing. Temperature changes under light-colored bark such as that of birch, poplar, etc., are much less marked than under dark-colored bark, and

whitewashing fruit trees is a common method of reducing or preventing sun scald.[227]

The internal temperature of pine needles in sunshine and in still air during winter has been found to be as much as 18°F. higher than that of the surrounding air.[152] Many buds and densely hairy leaves are examples of aerial parts that exhibit considerable influence in retarding the transmission of heat because of the nature and condition of their surfaces. Rough surfaces absorb and radiate a greater proportion of energy rays than do smooth ones. The color is highly important, red leaves, for example, absorbing more heat than green ones and the white portions of variegated leaves least of all.

The heating effect of direct sunshine upon green leaves is limited not only by the loss of heat by conduction and radiation but also by the cooling effect of transpiration. Even in intense sunshine the temperature of turgid, rapidly transpiring leaves is usually below that of the surrounding air.[101, 474] The cooling effect of transpiration may be shown by comparing the temperatures of vigorously transpiring leaves with those of dead ones. In the case of corn, differences of 8.5°F. have been found in the sun.[280]

In taking the internal temperatures of plants, such as thick stems, roots, large buds, or other bulky parts, a thermometer with a small, flat bulb is useful. A small slit is cut or a hole made with a small cork borer and the bulb sunk into the tissues. Temperature readings are less easily obtained in the case of ordinary leaves. Approximate differences in temperature between air and leaf may be made by rolling the leaf while in position tightly about the thermometer bulb. But for exact readings, thermoelectric methods for the determination of leaf temperatures must be used.[475]

To Compare the Temperature of Plants with That of the Surrounding Air.—Bore a small hole in the stem of a cactus, leaf of Agave, bud of horse-chestnut, potato tuber, or other bulky plant part. Insert a small thermometer with flattened bulb that is only about 2 millimeters wide and 1 millimeter thick. Determine the temperature of the plant part and that of the surrounding air. Remove the plant (or part) to a very much colder or warmer place and ascertain how long a period of time is required for the living organ to take on the temperature of the air. Do fleshy roots have the same temperature as the surrounding soil? What are the causes for the difference between plant and air or soil temperatures?

Bore a hole, just large enough to receive the bulb of the thermometer, tangentially under the bark of a tree on both the sunny and the shady side. Carefully insert the thermometers and seal them in place with modeling clay. What differences do you find in temperature? Why? Compare that of trees with light- and dark-colored bark of about the same thickness, *e.g.* birch and cherry.

Variations in Temperature.—As in the case of light, there is a daily and an annual fluctuation in temperature. The amount of heat received depends upon the angle of the sun's rays and their consequent absorption.

The actual temperatures at the surface of the earth are greatly modified by radiation, conduction, and convection. In consequence, the maximum daily temperature does not occur at noon "sun time," as in the case of light, but somewhat later, often about 2 to 3 p.m. The minimum is not reached at nightfall, but just before sunrise upon the following morning. The maximum temperatures for the year do not occur at the June solstice, but a month or two later. Similarly, the minimum falls a month or more after the December solstice.

Variation of temperature occurs with changes in latitude and altitude. Northern latitudes receive the sun's rays at a greater angle than southern ones, and the absorption of heat by the atmosphere is correspondingly greater, thus leaving less for the soil surface. In so far as absorption is concerned, high mountains receive more heat than lowlands. The loss by radiation, however, is so much greater that mountainous regions are uniformly colder than plains or lowlands lying on the same parallel. This is due to the rarity of the air, which allows heat to pass through it readily. Although the air on mountain tops is colder than that of the plains, the surface temperature of the soil is often considerably higher. On Pike's Peak the surface of the soil may show a temperature of 140°F. while the air 5 feet above is 70° and the soil 10 inches below the surface 55°. This difference, however, is far overbalanced by the rapid radiation at night.

Temperature also varies with the slope. This is due to the fact that a square decimeter of sunshine covers this amount of surface only when the rays strike at right angles. As the angle diminishes, the rays are spread over more and more surface until at an angle of 10° a square decimeter receives but 17 per cent as much heat as at 90°. This has more effect upon soil temperature, humidity, etc., than on the plants directly, owing to the fact that stems and leaves have the same position upon a slope that they do upon the level. Furthermore, temperature differs at various levels in the air and the soil. Air and soil temperatures naturally affect each other. The highest temperatures are usually found between the two, *i.e.* at the surface of the soil. In summer, the temperature rapidly decreases in both directions. In the air, this is due to the fact that radiation becomes imperceptible a short distance above the ground, while the influence of the wind becomes more and more noticeable. Heat penetrates the soil slowly, either on account of poor conductivity or because of the great capacity of the water for latent heat. The air is ordinarily warmer in the daytime than the soil, especially on sunny days. It loses heat more rapidly, however, and after a sudden decrease in temperature or at night the soil is usually for a time warmer than the air.

Influence of Other Factors.—Many factors exert a marked influence upon temperature, among which (1) clouds and wind are, perhaps, most important. During the day, clouds reflect a considerable portion of the

insolation from their upper surface, and, consequently, the temperature at the surface of the earth is decreased. At night clouds intercept heat radiated from the earth and, in consequence, the temperature of the surface soil and the air in contact with it is lowered but little. Hence, in spring and autumn, frosts are not likely to occur during cloudy weather. Fogs, high humidity, a cover of scrub or forest growth, and, in fact, anything that retards direct insolation by day and solar radiation by night, have a similar effect in making the temperature of the habitat more uniform. Cover, whether dead or alive, reduces day temperatures by screening out the sun's rays and increases night temperatures by retarding radiation. It is for this reason that forests and scrub are cooler

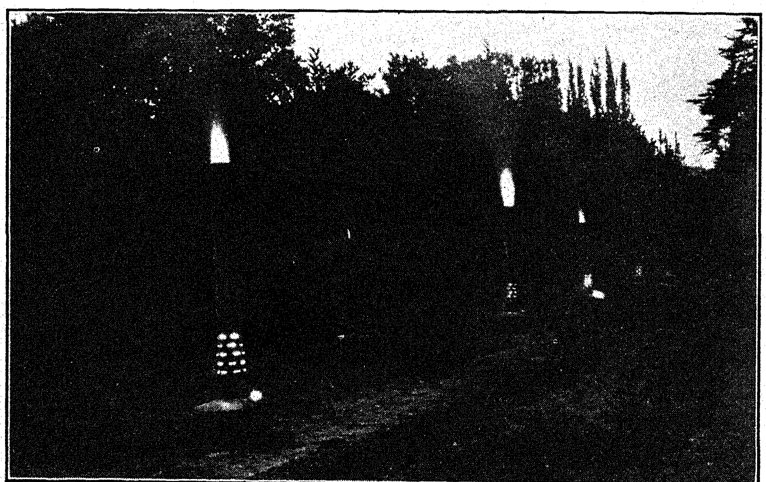

Fig. 154.—Orchard heaters in operation in a California citrus grove. (*Photo by U. S. Dept. Agr.*)

in summer and warmer in winter than other areas that are similar except for cover.

Winds cause the temperature to rise when they blow from a warmer region and to fall when they come from a cooler one. On clear, still nights in early spring in temperate regions, frosts are likely to occur which destroy the early vigorous growth, especially that of cultivated plants. The end of the growing season may be similarly shortened, especially for annuals, by early frosts in autumn. But on windy nights where the heavy, cold air is prevented from settling to the ground and constantly mixed by winds with the warmer air, freezing is much less frequent. Since the surface of the land warms up in sunshine about four times as rapidly as that of water and cools much more rapidly at night, the stabilizing effect of large bodies of water, *e.g.* the Great Lakes, on temperature of adjacent land is obvious. Such areas are often well

adapted for fruit growing, since spring opens late, after danger of frost has largely passed, and early frosts in fall are uncommon.

Valuable orchards are often protected from damage when frost is imminent by building numerous smudge fires which surround the trees with artificial clouds of smoke, or, more usually, by the use of charcoal or oil burners (Fig. 154). These not only add heat to the atmosphere but also especially cause convection currents that keep the entire mass of air more or less thoroughly mixed. Such procedure is especially effective on still nights (Fig. 155). Truck crops are often protected in a similar

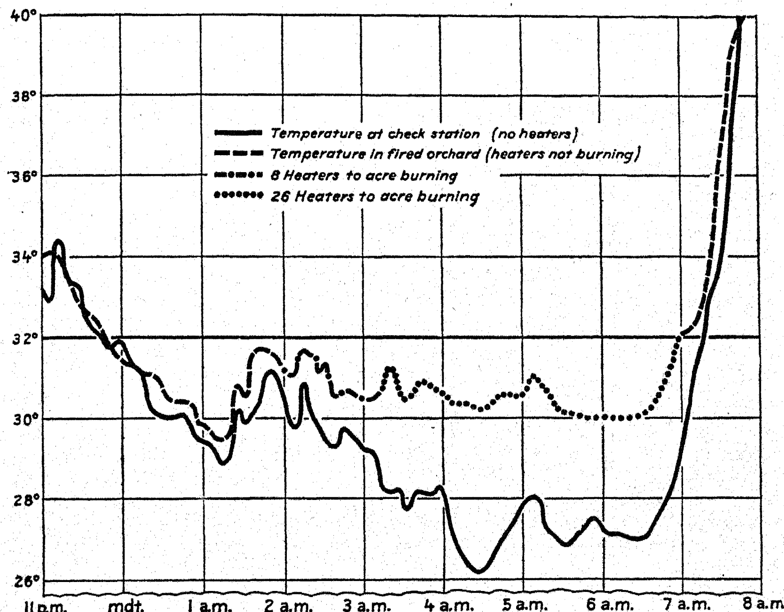

FIG. 155.—The rise of temperature as affected by heaters and fires placed in orchards. (*After Corbett, et al., U. S. Dept. Agr.*)

manner or by preventing radiation by a suitable covering of paper, cloth, etc.[116]

Soil temperature, which modifies the air above the surface, is greatly affected by the water content and also by the color of the soil. Wet soils, because of the high specific heat of water, warm slowly, and especially if they are light in color. Thus, a wet soil, such as a marsh, lowers the air temperature, partly by increasing humidity which, in turn, decreases insolation. In such low areas, frosts are especially frequent and severe.

The effect of exposure is closely connected with slope. Slopes that face south and west receive the most sunshine and are regularly warmer than north and east slopes. Hence, in mountainous regions, forest communities, whose upward extension is directly or indirectly limited by temperature, may occur much higher on warmer slopes.[22,383] Lodgepole pine

(*Pinus contorta murrayana*), for example, is generally found in Colorado between altitudes of 8,000 and 10,000 feet. But on warm, south slopes it may extend as high as 11,000 feet and as low as 7,500 feet on cold north

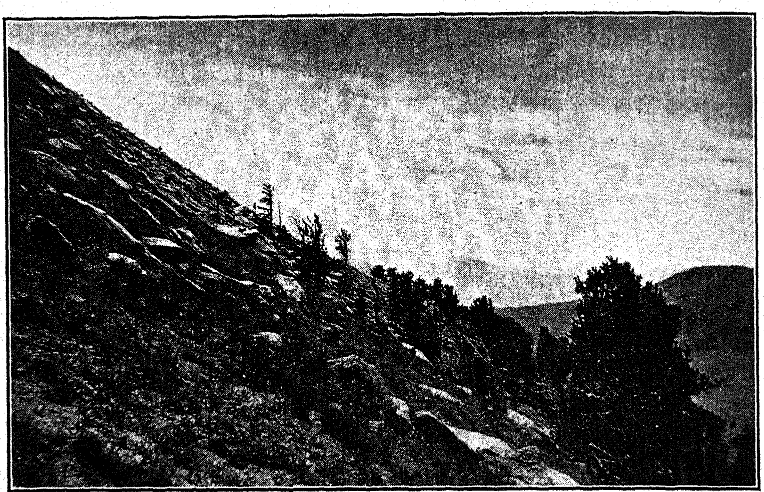

FIG. 156.—Timber line on the east side of Pike's Peak at about 11,000 feet altitude. The forest consists of Engelmann spruce (*Picea engelmanni*) and limber pine (*Pinus flexilis*). (*Photo by Pool.*)

ones.[410] Timber line, *i.e.* the uppermost extension of forest growth, is often 1,000 feet higher on south than on north slopes[483] (Fig. 156). In general, the larger the mountain mass and the higher the mountains the greater the altitude to which the tree limit attains (Fig. 157). Yellow

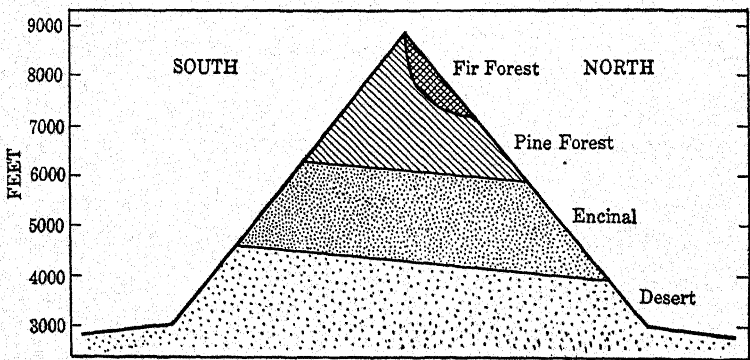

FIG. 157.—Effect of slope on distribution of desert vegetation, oak woodland, yellow pine, and Douglas fir forest in the Santa Catalina Mountains in Arizona. (*After Shreve.*)

pine (*Pinus ponderosa*) may extend far upward into the Engelmann spruce (*Picea engelmanni*) zone on dry, well-insolated slopes, while the spruce follows the deep canyons almost down to the plains where the canyons are watered by cold streams and subject to cold-air drainage.

In growing fruit trees and other crops in regions of rough topography, careful account should be taken of the slope and temperature relations. Strawberries may be brought to bearing many days earlier if planted on a south-facing slope where both soil and air are warmer. North slopes may be selected for orchards to retard blossoming and consequent damage by late frosts.[9]

Temperature Inversions and Cold-air Drainage.—In hilly and other rough lands, a well-marked, local temperature effect is often noted in valleys or depressions into which the denser, cold air sinks at night during the summer. On bench lands and the upper slopes of table-lands, the average temperature may be 6 to 10°F. or more above that of the valley bottoms below, which during the day are warmest.[19] Such temperature inversions are particularly effective on cold, calm nights and in arid or semiarid regions where there is little cover to prevent rapid radiation. Sometimes the line of temperature variation between the layer of cold air below and warmer air above may be so marked that blossoms on the lower part of a tree will be frozen while those above escape freezing and form fruit abundantly. This settling of the colder air is termed cold-air drainage. It often creates distinct air currents as it pours down mountain canyons by night. Sometimes, certain species or communities of plants are limited in their upward distribution to the warmer exposed ridges but do not occur in the area subject to cold-air drainage. Timber line on mountains is profoundly modified by the effects of cold-air drainage, as a result of topography.[479]

Temperatures Favorable and Unfavorable to Plants.—Plants are adapted to a wide range of temperature. Some species are able to grow in extremely low or extremely high temperatures as long as water is available in the liquid form. In fact, some of the lower forms of plant life such as algæ may grow and fruit in Arctic waters at temperatures below zero, the salt of the ocean lowering several degrees the temperature at which the water congeals. Conversely, numerous algæ and bacteria thrive in hot springs at temperatures as high as 77°C. and a few fungi can endure temperatures of 89°. In general, the temperatures of the plants' own habitat are most favorable to their development. For tropical plants, air temperatures above 90°F. are most favorable. Most temperate plants make their best development between 60° and 90°, while Arctic and alpine species grow at temperatures only slightly above the freezing point.

Plants are subjected to a considerable range of temperature during their period of growth. They grow only when the temperature remains within certain limits and mature and die or become dormant when it falls too low or becomes too high. Thus, low temperatures enforce a resting period upon plants of temperate and boreal regions just as there is a resting period for vegetation in climates where there is at certain periods an

insufficient water supply to meet the demands of transpiration. In both cases the response is the same. The plant reduces water loss by shedding its leaves or in other ways, and life activities are maintained at a low rate.

Optimum Temperatures.—The temperature at which a plant functions best is called the optimum. Optimum temperatures for the various physiological processes, *e.g.* photosynthesis, respiration, reproduction, etc., are themselves difficult to delimit because each depends upon a group of physical and chemical factors any one of which may limit a particular process. In general, the various optima for the different physiological processes do not coincide, that for respiration, for example, being much higher than the optimum for food manufacture. Hence, it seems clear that the ecological optimum or temperature at which the plant as a whole develops best is never a mere point but a range of several degrees at least. As the chemical and physical processes within the plant are quickened by a favorable temperature, demands for water and nutrients are also increased. Only when these are abundant do there occur optimum conditions for metabolism and growth. For germination and seedling development these are much lower than those for the fruiting plant.

Maximum Temperatures.—The maximum temperature that can be tolerated without injurious effects in the plant, often resulting in death, varies greatly with the species. It seems to be an inherent quality of the protoplasm, fixed as a result of the impress of certain temperature relations throughout untold generations. Such temperatures are very closely connected in nature with alterations in the water relations, *i.e.* available water supply to the roots and the cooling effect of water loss from leaves and shoot, and these become almost hopelessly confused with the temperature effects. At high temperatures, because of water or other relations, the growth rate rapidly falls and soon a point is reached beyond which the plant dies. At about 40°C., changes begin to occur in the protoplasm that are inimical to the life of the plant, and many plants succumb at temperatures a few degrees higher.

Like minimum temperatures, maximum ones vary widely with different species. Some tropical plants carry on their life processes at temperatures so high that most plants if subjected to them would die in a very short time. Furthermore, a plant withstands extremes of heat and cold much better in some stages than in others. It is least resistant in the active condition when the tissues are filled with water and most resistant in the resting state typical of spores, seeds, corms, etc. When dry, seeds can endure temperatures above 100°C. although they are readily killed at 70° if water-soaked. Certain species of yeasts have been shown to be capable of enduring a temperature of 114° when dormant, and bacteria in the spore condition are able to withstand temperatures of 120° to 130°C.

Minimum Temperatures and Freezing.—The minimum temperature at which any plant can continue activity is approximately the freezing point of water. Some Arctic and alpine plants (*e.g.* marsh marigold, *Caltha;* dogtooth violet, *Erythronium*) may produce their flowers after coming up through banks of snow and continue to flourish, although the temperature falls below freezing every night. The activities of marine algæ at temperatures below zero have been mentioned. On the other hand, many tropical plants are retarded in growth at 20°C. and are frequently killed at 10°. The minimum temperature, moreover, varies greatly at different times of the year and with different conditions of the plant as well as with its previous experience with low temperatures.[513,594] The chief difference lies in the amount of water the plant contains. The watery leaves and herbaceous stems of plants of temperate climates, for example, are usually killed by an exposure to 0°C. and frequently at temperatures 2° to 4° above freezing.[458] The drier seeds and inactive underground parts resist the long continued effect of temperatures of −30° to −40°C. Death by winterkilling or cold at any time is really a matter of desiccation and its attendant results brought on by low temperatures.

Since the cell sap always contains solutes that depress its freezing point, only temperatures lower than 0°C. cause the water to congeal. Plant tissues can be undercooled several degrees below the freezing point and warmed up again without injury provided no ice formation occurs.[593] A plant or its growing parts (buds, cambium, etc.) are not necessarily killed, even though they are solidly frozen. Arctic explorers on the coast of Siberia report plants, such as certain mustards (*Cochlearia*), being overtaken by winter and exposed to extremely low temperatures (−46°C.) while still in the flowering stage. In spite of this, they began again to blossom quite unharmed upon the recurrence of warm weather.

To Observe the Appearance of Ice Crystals in Buds.—On a cold day in winter when the temperature is 15°F. or lower, cut sections of buds of white birch (*Betula alba*), red elm (*Ulmus fulva*), or lilac (*Syringa*). This must be done in a place where the temperature is well below freezing and the sections mounted in cedar-wood oil so that the water from the melting ice can not evaporate. Immediately examine them under a microscope that has been thoroughly cooled. Note the crystals of ice between the bud scales which they have more or less pushed apart. Observe closely the changes as the ice slowly melts and the spaces in which the ice is collected shrink as the water is reabsorbed by the cells.

Nature of Freezing Injury.—When plant tissues freeze, water is withdrawn from the cells much as it is when they wilt, and crystals of ice form in the intercellular spaces. This explains the flaccid condition often observed in frozen plants. The film of pure or nearly pure water on the outer surface of the cell wall freezes first. Water is then withdrawn from within the cell wall, next from the protoplasm, and finally from

the cavities or vacuole to replace this film. It is the force of crystallization that causes the water to move outward. After equilibrium is established between this force and the water-retaining power of the cell at any temperature, no more water freezes unless the temperature becomes lower.[585] It seems almost certain that death is not due to cold but to the results attending this process of desiccation. Whether the cells are killed directly by loss of water on freezing or by changes taking place as a result of this water loss, the rate of thawing has no effect, since they are already dead. But among plants capable of standing some ice formation in their tissues, slow thawing is least harmful, since it enables them to reabsorb much of the water that has been withdrawn into the intercellular spaces that might be lost if thawing were rapid.[80,81,412]

The result of withdrawal of water from the cell is a greater concentration of the salts within. This may be accompanied by an increased H-ion concentration. Certain proteins are precipitated in strong salt solutions, and it is generally believed that the chief cause of injury or death by freezing is the precipitating of proteins from the desiccated protoplasm. For example, it has been shown that approximately one-third of the proteins in frozen plants of cereals are precipitated. In the tender begonia, protein precipitation occurs at $-3°$C.; in winter rye, at $-15°$; and in pine needles, not until a temperature of $-40°$ is reached.[192]

Resistance to Freezing.—Water-imbibing substances and osmotic pressure decrease the outward movement of water from the plant cell. In general, it has been found that plants and tissues with the greatest water-retaining power are also the most resistant to both freezing and drought. Hence, it is rarely the youngest tissues or parts that are injured by freezing. In winter wheat, for example, injury progresses in a given plant from the older to the younger leaves, and the crown containing the dense protoplasm characteristic of meristematic tissues is the most hardy.[333] In northern latitudes, most evergreen trees, shrubs, and herbs, as the temperatures become lower, convert their reserve supply of starch into fats and oils. This also occurs in certain deciduous trees like the birch. It is well known that water in the presence of fatty oil in the form of an emulsoid may be much undercooled before ice formation takes place. Moreover, in many cases, an abundance of sugar occurs in the cell sap.

A consistent increase in the osmotic pressure of the cell sap of evergreen trees and shrubs with decrease in temperature during fall and winter has been demonstrated[174,311] (Fig. 158). This further decreases the freezing point of the water, and the danger arising from the salting out of the proteins is further minimized. During freezing or as a result of freezing, sucrose may be changed to the reducing sugars and the osmotic efficiency consequently greatly increased. The presence, moreover, in the cell of these non-electrolytes decreases the tendency to precipitate proteins.[365]

Pentosans, mucilages, and pectic bodies, which have a high water-retaining power, are abundant in many plants and further decrease the danger from desiccation and consequent death. In the living leaves of *Pyrola*, a typical evergreen herb of boreal forests, ice formation does not begin until a temperature of −31°C. is attained.[545]

Thus, as a result of various modifications of metabolism and protoplasmic content resulting from long experience with periodically low temperatures, plants have become adapted to freezing by their ability successfully to resist desiccation. In fruit trees, such as plums, for example, it has been demonstrated that while the hardy varieties may not have a higher water content than the non-hardy ones, the buds are

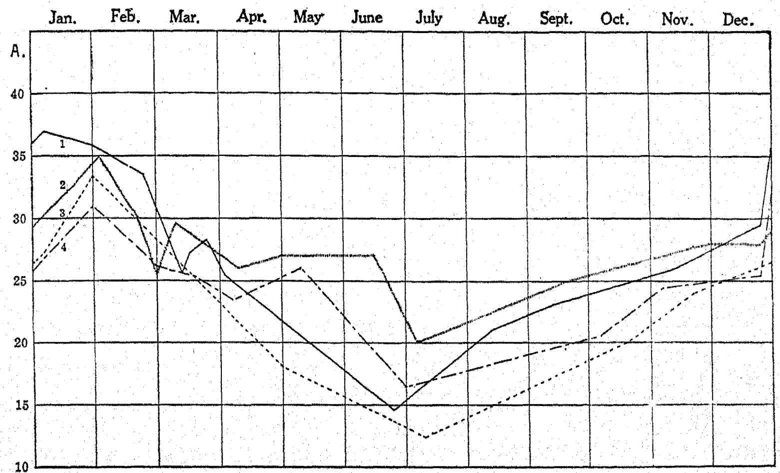

FIG. 158.—Increase in atmospheres of osmotic pressure of cell sap in leaves of evergreen plants in Idaho during fall and winter and decrease during spring and summer: 1, white fir (*Abies grandis*); 2, Douglas fir (*Pseudotsuga mucronata*); 3, a shrub, *Pachistima myrsinites*; and 4, yellow pine (*Pinus ponderosa*). (*After Gail.*)

able to retain a nearly uniform water supply under conditions of extreme cold (drought), while the non-resistant varieties become desiccated and die. In the "hardening" of plants, similar changes are produced.[517]

Hardening.—Hardening is a term applied by gardeners and other plant producers to the practice of rendering plants less susceptible to drought and frost injury. Seedling vegetables grown in a greenhouse or hotbed are very susceptible to drought and freezing. If they are placed in a cold frame for a few days at a temperature several degrees above freezing and watered sparingly before setting into the field, they increase in hardiness to a point where some varieties will withstand frost. In fact, certain varieties, such as cabbage, may be frozen stiff without injury. The hardening process in plants is accompanied by a marked increase in the water-retaining power of the cells that enables them upon freezing to retain a large proportion of their water content in the unfrozen state.

This is associated with a decrease in total water content; an increase in the amount of hydrophilous colloids, such as pentosans, together with an increase in their power to hold water; and an increase in the amount of osmotically active substances such as sugars. Other important changes also occur. The proteins of the protoplasm are changed to forms that are soluble in water and less easily precipitated.[412] For example, by subjecting the expressed sap of non-hardened and hardened cabbage to a temperature of $-4°C.$, a temperature that would kill the non-hardened cabbage but not the hardened plants, it was found that 31 to 44 per cent of the proteins in the former were precipitated but only 9 to 11 per cent of the latter.[226]

The first three changes mentioned above may take place in a relatively short period of time when the activity of the plant is limited by cold or drought; the last is important only in plants hardened by prolonged exposure to cold. Hardy species and varieties of plants possess the ability to initiate these changes to a greater or lesser degree; while non-hardy ones possess it only to a slight degree or not at all.[412] Winter wheat, for example, hardens readily, and certain varieties can withstand drought and extremely low temperatures, but oats seem to lack this ability and are resistant neither to drought nor to low temperatures.

Some plants may be hardened by subjecting them to drought before the advent of freezing. It is a common practice among foresters thus to harden seedlings in nurseries, and similar results may be obtained by withholding water in orchards, if under irrigation, or otherwise by the use of appropriate, late-sown cover crops. The changes in the cell are similar to those brought about by hardening due to low temperatures. Perennial plants, in general, are much less likely to be winterkilled if they undergo a period of moderate drought than if they are kept wet and green up to the time of severe freezing. The hardiness of some plants, *e.g.* certain varieties of peaches, is due to the slowness with which they absorb water in spring. The sap in the buds remains at such a high concentration that they are not readily injured by freezing.[267]

The Sum of Temperatures.—The activity and growth of any plant depend upon its receiving the requisite amount of heat during the growing period. The influence of temperature on the size of the plant is very great because of its control over growth. The sum of the temperatures that act upon a plant is of the first importance in determining its general appearance. The effect may be produced either by temperatures that are more or less constantly too low or by shortness of season, which is equally effective in reducing the total amount of heat available for the use of the plant. As a rule, these two factors act in unison and produce marked reduction in size. Such reduction is characteristic of the vegetation of alpine regions, although the dwarf habit of alpine plants is chiefly due to adjustment to water, absorption being retarded by a cold soil

and transpiration promoted by a rarefied atmosphere (Fig. 159). The general effect of low temperatures may be seen in field crops during seasons in which the temperatures are largely below the normal. It may also be readily demonstrated by growing seedlings of the same species in warm and cold compartments of a greenhouse.

Since temperature is one of the most influential of all climatic factors affecting plant growth, it has received much attention in connection with crop production. In spite of much study, very little is known about the relationship between air temperature and the development of any crop.

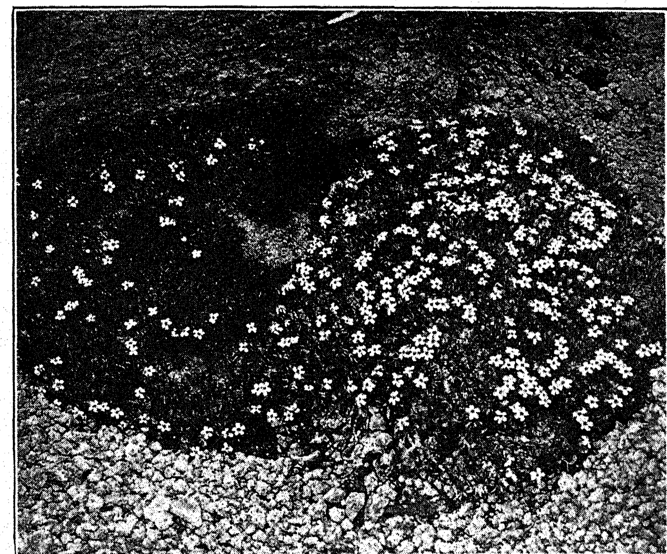

Fig. 159.—Alpine mats of moss campion (*Silene acaulis*) growing on the north side of a rock. The effect of different temperature sums is shown by the number of flowers.

Could the heat requirement of various crops be stated in terms of temperature and time, it would be of immense advantage to agriculture.[456]

For many years, an effort has been made to determine the total of the effective heat units necessary to grow various crops to maturity. Since all temperatures below the minimum are ineffective in promoting growth, it was first necessary to select a plant zero, *i.e.* a temperature above which growth begins. Since this varies for different crops and, to some extent, with other conditions such as latitude and altitude, length of day, etc., different plant-zero points have been suggested, such as the mean daily temperature of the average date of planting.[282,284] The latter is about 37°F. for spring wheat, 55° for corn, and 62° for cotton. It varies but little, regardless of where the crop is grown. The plant zeros most used, however, have been 43° and 40°F., and three summation processes

have been employed to determine the effect on plant growth of temperature sums above this point.[319]

Remainder Indices.—By the process of remainder indices of temperature efficiency for plant growth, which has been used most frequently, all mean daily temperatures above the plant zero during the life of the crop have been added together. This would be 10° for a day with a mean temperature of 53°F.; 15° for one with 58°; etc. Obviously, a degree of heat at 60°F. is of much more value in promoting growth than one at 50°. Hence, it is not surprising that the total units for a given crop in a particular region vary so widely that they have little significance. The heat units for corn in Ohio during a period of 27 years varied from 1232 to 1919 from sprouting to flowering, and from 897 to 1607 from flowering to ripening.[456]

Merriam's division of the United States into life zones and crop zones is based upon the sums of heat thus determined, together with the mean temperature for the 6 hottest consecutive weeks. The sums thus obtained at various stations were plotted and connected by isothermal lines. The United States was thus divided into various life zones. The transition zone, for example, has for its northern boundary lines connecting stations with heat sums of 10,000°F. (northern parts of Minnesota, Wisconsin, and New York), while its southern boundary is along a line with 71.6°F. for the 6 hottest weeks (northern parts of Iowa, Illinois, and Maryland). From the standpoint of natural vegetation, this classification is necessarily unsatisfactory, since temperature is far less critical than water to native species. For example, it places such diverse vegetational units as climatic grassland, yellow-pine forest, and sagebrush desert in the same subdivision of a zone, *i.e.* arid transition. The conclusions reached by this author have been largely adopted by many of the earlier students of plant and animal geography, despite the exceedingly tentative nature of the data on which they are based. The zonal terminology has, moreover, been so widely used that the student will do well to familiarize himself with it.[349]

Exponential Indices.—Exponential indices of temperature efficiency for plant growth are based on the fact that the physiological processes of plant metabolism are chemical and physical and follow the principle of Van't Hoff and Arrhenius. This principle states that the chemical-reaction velocity approximately doubles for each rise in temperature of 18°F. On this basis, indices of temperature efficiency have been calculated, assuming that general plant activity occurs at unity rate when the daily mean temperature is 40°F. and that this rate is doubled with each rise of 18°F. in the daily mean. Thus, with a daily mean of 58° the rate becomes 2, with a mean of 76° it becomes 4, etc. Hence, the index of efficiency I may be found for any temperature t by substituting in the formula $I = 2^{\frac{t-40}{18}}$ (*e.g.* that of 94° would be $2^3 = 8$).[319] Increasing

temperature is not accompanied by increased growth throughout the range of the growth rate from the minimum to the maximum. Instead of the growth of wheat, for example, doubling at 100° that which occurred at 82°F., it actually decreases. An optimum temperature can always be found above which the previously increasing growth rate begins to decrease.

Physiological Indices.—Physiological indices of temperature efficiency for plant growth take into account the optimum temperature. The method is of such a nature that both low and high temperature values give efficiency indices of zero, and intermediate temperature values give indices whose graph shows a well-defined maximum. Variations in the growth rate of corn seedlings were experimentally determined at different constant temperatures of long duration.[307] From these, the efficiency index for each degree of temperature between 36° and 118°F. was calculated. For example, the value at 36° is 0.1; 40° is 1.0; and 58° is 16.1. At 89° it reaches a maximum of 122.3 and falls again to 0.1 at 118°F. This method is more promising than any of the preceding and as a laboratory experiment and a basis for ecological investigation the information obtained is of great value.[315] In nature, however, any one temperature is not long maintained. Care should be taken in applying the results to plants in the field, and maps of temperature efficiency and provinces constructed on these bases, as their authors realized, can be considered scarcely more than suggestive. Finally, it must be remembered that temperature is only one of a series of a complex of environmental factors that affect plant growth.

Influence of Temperature on Vegetation.—There are probably few places on the surface of the earth that are either too hot or too cold for some plants to grow. Even in boreal regions, the temperature in summer is always well above the limits at which growth is possible, although this period may extend over only a few weeks. Consequently, many species, especially annuals, are excluded. Plants of alpine and high Arctic regions are almost exclusively low-growing perennials in which rapid growth is due to utilization of food accumulated the previous season. Similarly, plants of the hottest deserts, where continuous growth is limited by extreme heat, have living parts buried deeply in the soil. Upon the advent of a moist or rainy season, when the temperatures are reduced and water becomes available, they draw upon their reserve food supplies and rapidly develop.

Temperature has no effect upon plant distribution as regards migration, but it has a profound influence upon ecesis of the migrants.[538] Considering temperature alone, ecesis is more certain if the migration is east or west than if it is northward or southward. Generally, also, the chances for ecesis are greater southward than they are northward. Migration to the east or west does not essentially change the relation

of the plant to temperature. Migration southward means that the plant must accustom itself to higher temperatures as well as to greater annual sums. Maximum temperatures may be directly operative in preventing the extension of plant ranges, the temperature of the soil surface and of the air just above being especially important. While adjustment to higher temperatures is taking place, the plant may be at a disadvantage in competition with others already well established.[426]

Plants that migrate northward, in addition to a corresponding adjustment to lower temperatures and a lower sum, run an increasing risk of encountering a fatal minimum. This risk is greatly increased by the fact that southern plants require a longer period for their life cycle than northern ones and in a northern latitude are often unable to reach maturity before the regular appearance of killing frosts. The evergreen habit is clearly advantageous where the growing season is very short, none of the very restricted period during which temperature is high enough for photosynthesis being squandered in the production of a new canopy of foliage.[385] Such species occur regularly in cold climates and at high altitudes. It frequently happens that the limiting condition preventing the occurrence of certain species in an area is the nature of the surroundings during a dormant period. In fact, it may be found that the length of the dormant period during which growth can not occur is as important in plant distribution as is the duration of the growing period itself.[482] Even dormant plant protoplasm may be destroyed at extremely low temperatures.

The same fundamental rule of distribution applies to mountains, the increasing cold upward makes ecesis more uncertain than it is downward. The grouping of species, which is a process in the formation of vegetation, is in accordance with these facts. In consequence, vegetation exhibits zones extending east and west upon continents. The isothermal lines are usually deflected southward with increase in altitude. This occurs on either side of the three main mountain systems of North America. They bend northward near the Atlantic and Pacific oceans. Along mountain ranges the zones are, in general, lengthwise of the range, although many minor factors such as the extent of the mountain masses, slope exposure, air currents, proximity to bodies of water, etc., interrupt a regular distribution.[212]

While temperature is the most important factor in determining the general distribution of vegetation, its effect is much greater upon the flora than upon the kind of vegetation. Grassland, forest, and desert all occur in each of the great temperature zones of the earth, but the component species of forest, for example, in each zone are very different. Temperature also is the most important factor in determining the distribution of crop plants. The northern limit of the successful commercial production of cotton is determined almost entirely by temperature

conditions.[284] The isotherm of 10°F. for the daily minimum temperatures of January and February, for example, coincides, in general, with the northern boundary of winter-wheat culture in the United States, if this boundary is taken as the line beyond which spring wheat is grown more commonly than winter wheat.[428] Potatoes, on the other hand, give the highest yields in regions with the lowest summer temperature, since tuber growth is retarded by high temperatures. Temperatures of the growing season alone limit the growth of certain crops such as corn, while others, *e.g.* grapes, are limited by the temperature of the non-growing season as well. East of the Rocky Mountains, the agricultural areas have more or less distinct boundaries that correspond, in general,

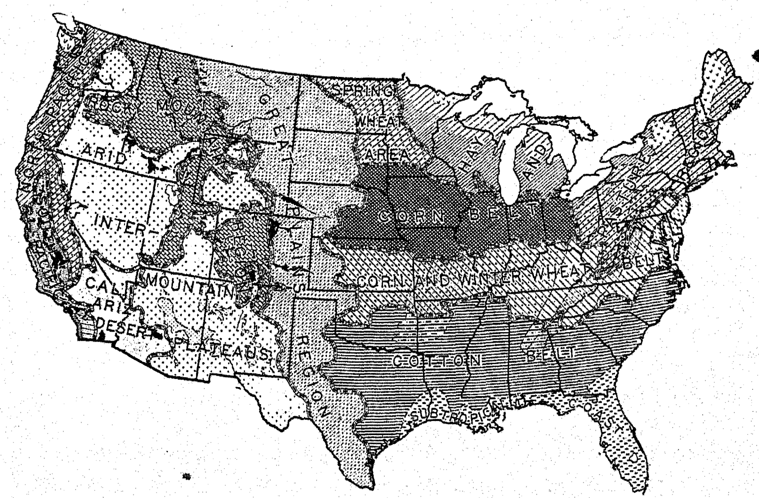

FIG. 160.—Agricultural regions of the United States. The six regions of the west have been given topographic and geographic names because of the dominating influence of topography and the Pacific Ocean. (*After Baker, U. S. Dept. Agr. Yearbook*, 1921.)

with the east and west trend of isothermal lines. The more important ones from south to north are the subtropical coastal belt, the cotton belt, the corn and winter-wheat belt, the spring-wheat area, and the hay and pasture region[16, 552] (Fig. 160).

Relation of Air Environment to Disease.—The close relationship that exists between temperature, humidity, and other conditions of the weather and plant disease has long been recognized.[249] So obvious is this relation to the relative damage to grain by rust or mildew that the grower often believes that unfavorable rainfall or temperature is the direct and only reason for this trouble.[272, 524]

Some diseases are due directly to unfavorable environmental factors, for instance, tipburn or sun scald to high temperatures, and russeting of apples and pears to high humidity. The latter, for example, results from a cracking and weathering away of the epidermis of the fruits and an

increased development of corky parenchyma beneath. It occurs especially in humid climates or during rainy seasons and is due entirely to high humidity. In dry climates, under irrigation, the fruit is smooth skinned, since russeting does not occur.[176] The great majority of plant diseases, however, are due to bacteria or fungi.

Excessive shade, whether due to clouds or to foliage, and high temperatures accompanied by wind, high humidity, and heavy dews are ideal conditions for the rapid dissemination and development of a variety of bacterial diseases. Under such conditions, fire blight of pear, caused by *Bacillus amylovorus*, often breaks out like a conflagration, spreading over whole orchards. Other bacterial diseases such as the black spot and canker of the plum, bean blight, and angular leaf spot of cucumber spread rapidly and become most destructive under conditions of cloudy weather and heavy dews. Black rot of cabbage likewise develops rapidly under similar conditions. During moist, warm autumns, bacterial diseases of the potato may destroy almost the entire crop over extensive districts.[496]

Weather conditions, to a large extent, also determine the spread and severity of fungus diseases of plants, since favorable moisture and temperature relations are necessary for spore germination and consequent infection of the host. Humid days in midsummer are absolutely necessary for bad epidemics of the late blight of potato caused by *Phytophthora infestans*. The control of carnation and chrysanthemum rusts in the greenhouse, if the spores are present, depends upon keeping the leaves free from moisture and maintaining a low humidity. The amount of rust on asparagus in California is directly proportional to the occurrence of dew. Cereal rusts are most destructive when the weather is damp and cool.

Relation of Infection of Cereal Rusts to Humidity.—Fill six 2.5-inch flowerpots with potting soil in good tilth. Plant 15 kernels of some susceptible wheat, such as Little Club or Marquis spring wheat in each. At the end of a week, or when the first leaf is nearly full grown, thin to 10 per pot by pulling out the other plants. Inoculate each plant with viable rust spores of *Puccinia graminis tritici*, by moistening the leaf and rubbing it lightly between thumb and finger and then transferring the spores to the wet leaf surface with a flattened needle.

Place two pots under a large, closed bell jar together with a glass of water, and two others under an open bell jar raised a centimeter from the greenhouse bench and containing also a glass of water. Put the remaining pots on the bench without cover. The plants should be transferred to their respective places immediately after inoculation and before the leaves dry. In case of bright sunshine, shade the containers and plants to prevent high temperatures.

Determine the humidity under each set of conditions at least twice during the 48-hour period of inoculation. This may be done by cutting a circular hole 5 millimeters in diameter in the center of a thick felt paper large enough to cover the bottom of the bell jar. Make a slit from the hole to the edge of the paper and insert a cog psychrometer just above the whirling device. A similar paper inserted from the opposite

side reinforces the first, and when the two are held against the bottom of the bell jar they close the latter while the humidity is being determined.

After 48 hours place all the plants, properly labeled, in a group on the greenhouse bench. At the end of 10 to 14 days cut away all but the original leaf and determine the percentage of rusted plants in each lot.

(Rust spores may readily be obtained in summer and an abundant supply maintained at all times by inoculating new host plants every 3 or 4 weeks.)

Brown rots of stone fruits are intimately associated with abundant precipitation and a humid atmosphere. A week or more of damp weather during the period of ripening of peaches, plums, or cherries may result in such abundance of the fungus that the entire crop over an extensive area may be ruined. Likewise, the fungus causing black rot of grapes is most destructive under similar conditions.

The destructiveness of the dry rot of potatoes caused by species of *Fusarium* gradually increases as the relative humidity is increased. With a high humidity at a given temperature, the rotting is always greater than at 5° to 10°C. higher with a low humidity.[193,303] Moisture and temperature play a leading part in determining the severity of apple scab, the disease being most severe where the climate is humid and cool in spring and early summer.

Environmental conditions may affect the various diseases quite differently. During a cool summer in southern Wisconsin, tobacco grown on "tobacco-sick" soil was practically a failure as a result of the excessive development of the root-rot fungus. But during a hot summer on the same soil, a good crop of fairly healthy plants developed. Conversely, the cabbage crop on old "cabbage-sick" soil during the cool summer was relatively free from "yellows," another parasitic disease caused by a soil-inhabiting fungus, while during the hot summer following, the disease practically ruined the whole crop.[272]

Explanation of the occurrence and severity of a parasitic disease requires not only identification of the causal organism but also the defining of the environmental factors favorable or unfavorable to its development. Because of the complexity of the environment and the continually changing combinations of factors, the latter is often the more difficult. Development of technique for determining the specific effects upon the metabolism of host and parasite of individual environmental factors is relatively recent, but much progress has been made and the outlook is promising.

CHAPTER XIII

LIGHT

Light is the direct source of energy for the manufacture of food. It is, therefore, an extremely important habitat factor. Next to soil moisture, it is the most important external factor affecting the form of plants and plays an important rôle in determining their structure. Light is that part of the radiant energy which is visible to the eye. It is from this radiant energy that chlorophyll absorbs certain rays or wave lengths which enable the plastids to manufacture food. Only a very small amount of the radiant energy striking the leaf is used in the photosynthetic process. In the case of *Polygonum*, *Tropæolum*, and *Helianthus* it was found to be only 0.42 to 1.66 per cent of the radiant energy available for photosynthesis.[58] Much of the radiant energy, including especially wave lengths longer than those visible, is absorbed and changed into heat energy. Of the total radiant energy incident upon a leaf, about 50 per cent is thus transformed and used in the vaporization of water; 19 per cent is lost by reradiation; and 30 per cent reflected from the surface of the leaf or transmitted through it.[508] Thus, the study of the effect of light upon plants and vegetation in general is greatly complicated because of the accompanying heating effect. The process of photosynthesis is conditional on temperature, the rate increasing, at the usual temperatures to which the plant is accustomed, according to Van't Hoff's law, provided no other factor becomes limiting. The rate approximately doubles with a rise in temperature of 18°F.

EFFECTS OF LIGHT ON PLANTS

The effects of light may be summarized as follows:

1. Production of chlorophyll.
2. Decomposition of carbon dioxide and the formation of carbohydrates.
3. Loss of water from chloroplasts and cells.
4. Changes in the number and position of chloroplasts.
5. Changes in the form and structure of the leaf.
6. Daily opening and closing of stomata.
7. Turning of stems and leaves.
8. Day and night position of leaves.
9. Effect on vegetative development and reproduction.

Production of Chlorophyll.—The primary response of the plant to light is the production of chlorophyll. This response does not occur in plants such as bacteria, fungi, brome rape (*Thalesia*), etc., in which the power to make chlorophyll has never been attained or has been lost in consequence of parasitic or saprophytic habits. On the other hand, certain plants, such as seedlings of some conifers, young fern fronds, and some one-celled algæ, become green in the absence of light.[377] Although formed in darkness, it can not function in synthesis of carbohydrates without light. With these exceptions, plants with plastids produce chlorophyll only in light, and the chlorophyll disappears in continued darkness.

The occurrence of chlorophyll beneath the outer bark in trees, however, indicates that only a small amount of light is required. The necessary light intensity varies in different species. In some, such as Norway maple (*Acer platanoides*) and peppergrass (*Lepidium sativum*), it forms in shaded habitats at less than three-tenths of 1 per cent.[606] At least over 1 per cent is required in temperate climates, however, for the species most tolerant to shade to carry on sufficient photosynthesis for growth. There is probably no place even in dense forests where plants can not form chlorophyll, but there are many places where even tolerant plants can not carry on photosynthesis, at least rapidly enough to live. For the majority of plants, sunshine or strong diffuse light presents the best condition for chlorophyll formation.

Influence upon Number and Position of Chloroplasts.—The clue to the internal structure of the leaf is found in the water relation. It has been seen that only a small amount of the radiant energy absorbed by the chloroplasts is used in photosynthesis and that a large amount is converted into heat, which produces vaporization of water in the cell. This process results in maintaining a lower temperature in the leaf. The effect is not so pronounced in the shade, owing to less insolation. In consequence, chloroplasts in the sunshine, where they are much more abundant, arrange themselves in line with the light rays and thus screen each other from the full effect of the radiant energy. This reduces the amount of water loss.

This arrangement does not seem to be a necessary protection against over illumination, for the chloroplasts of the guard cells receive stronger light without serious harm. It appears to be a device to prevent injurious water loss from the cell while the chloroplasts are active in food making. In the shade, the danger of excessive water loss is slight, while the need of obtaining all the light possible is imperative. Accordingly, the plastids, which are fewer in number, arrange themselves at right angles to the light rays, thus increasing the surface for absorption. This arrangement of the plastids is not only found in sun and shade leaves, but it is also typical of nearly all horizontal leaves (Fig. 161).

The movement of chloroplasts in response to light is a very general phenomenon throughout the plant kingdom. In the cylindrical cells of the filamentous algæ, *Mesocarpus* and *Mougeotia*, the large, flat chloroplasts come to lie with their surfaces at right angles to the direction of the incident light when this is moderate in intensity but turn "edge on" in intense light. Leaves owe the differentiation of the chlorenchyma

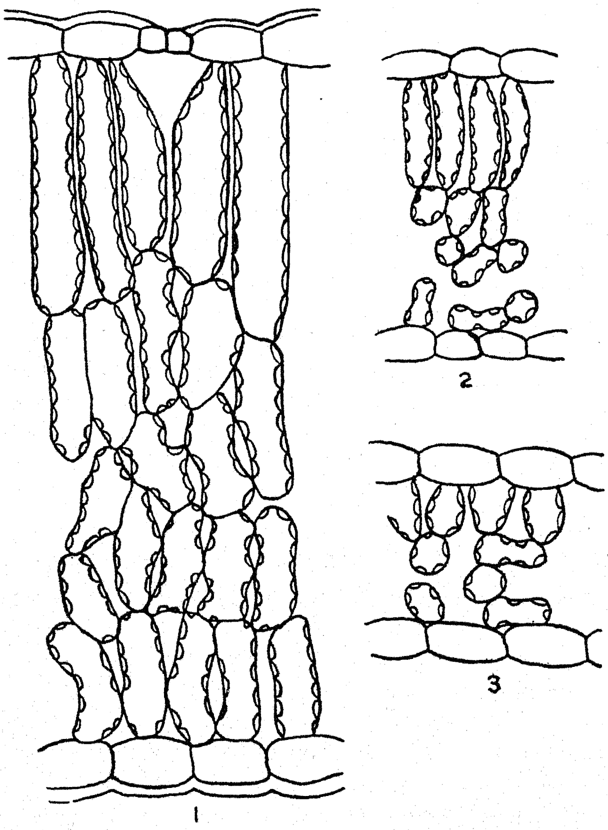

FIG. 161.—Position of chloroplasts in (1) sun leaf of narrow-leaved four-o'clock (*Allionia linearis*), (2) in a leaf of the shade form, and (3) in one found in very deep shade.

into palisade and sponge tissue to this fact. The upper part of the leaf receives full sunlight, and the plastids place themselves in line with the light rays. The lower portion receives only the light that is not absorbed by the upper. It is just as truly shaded as a leaf growing in a forest, and the chloroplasts spread out in such fashion as to receive as much light as possible. This arrangement is usual but it is not absolute, owing to local modifications due to the position of air passages and the necessity of the diffusion of water and solutes from cell to cell.

Changes in Leaf Structure.—The leaf undergoes the greatest modification as a response to light (radiant energy) of any organ of the plant.[86,228,399] Stems are modified to some extent, owing to the fact that they usually contain chloroplasts and bear the leaves. The root, not being exposed to the light, shows only indirect effects such as result from differences in growth due to an increased or decreased supply of photosynthate and the response to a well-lighted (hence, usually dry) or a moist, shady habitat.[222,512]

Changes in leaf structure brought about through the water relations, as affected by strong or weak illumination, are dependent primarily upon three facts: the number of chloroplasts increases with the intensity of the light; in diffuse light, chloroplasts arrange themselves in such a way as to increase the number exposed to light; under strong illumination, they orient themselves so that they decrease the exposure and the consequent water loss. The chloroplasts lie in the layer of cytoplasm that lines the cell wall. The wall itself is elastic and extensible and it surrounds a colloidal, jelly-like mass. The shape of the cell is, in consequence, very easily changed. The movement of the chloroplasts into lines or rows throughout the cell is probably the cause of its elongation in the direction of the rows. Hence, the formation of the palisade cells at right angles to the leaf surface is the normal result of the response of the chloroplasts to sunlight. The sponge cells, which elongate more or less parallel to the surface, are due to the action of diffuse light or shade upon the chloroplasts. The development of sponge tissues increases the light-absorbing surface. It is found in nearly all cases where the light is diffuse; leaves of shrubs and herbs that grow regularly in the deep shade of forest consist largely or entirely of sponge tissue. Cells that normally form palisade in the sun develop into sponge cells in the shade. Conversely, sponge cells under strong illumination develop into palisade.[87]

The amount of palisade developed in the upper portion of leaves receiving sunlight from above varies not only with the intensity of the illumination but also with available water content of soil. Palisade is much better developed in dry than in wet soil even under equal illumination. Moreover, where absorption is difficult because of poor root development due to low soil temperatures, palisade development is promoted. This is well illustrated by many alpine plants. Owing to low atmospheric pressure and consequent low humidity coupled with intense illumination in the habitat, water loss is excessive compared to absorption. Similarly, in plants growing under conditions of deficient aeration, excess of acids or alkali, palisade development is promoted.[540] It reaches its maximum development in very dry, exposed situations such as deserts. Here, because of dry soil, absorption is relatively difficult, while low humidity and high illumination promote excessive water loss.

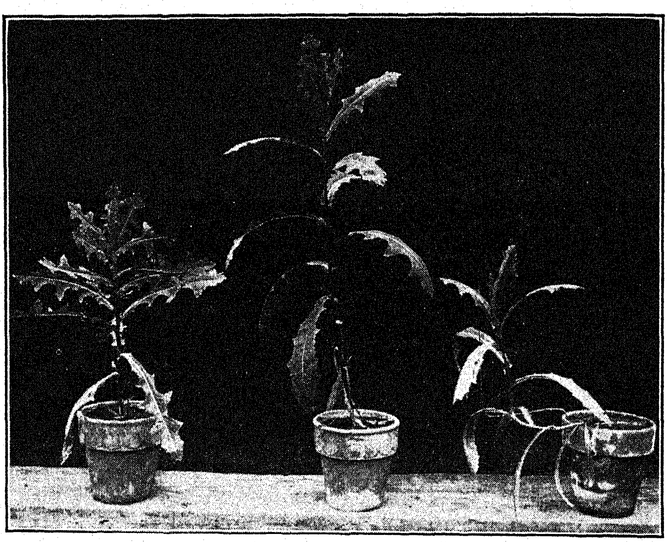

FIG. 162.—Prickly lettuce (*Lactuca scariola*) grown under full greenhouse light (left), 25 per cent of this (center), and 10 per cent (right).

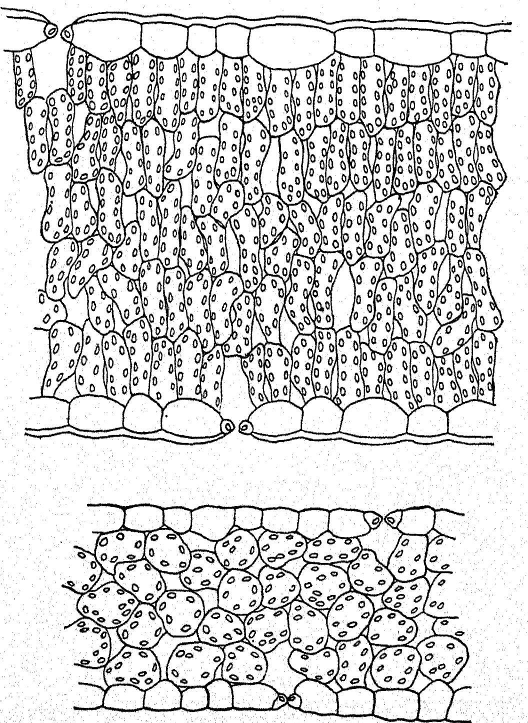

FIG. 163.—Cross-sections of leaves of plants shown in Fig. 162 grown in 100 per cent (upper) and 10 per cent greenhouse light.

Where the under surface of the leaf is also highly illuminated, for example by the reflection of light from white sand, palisade also develops

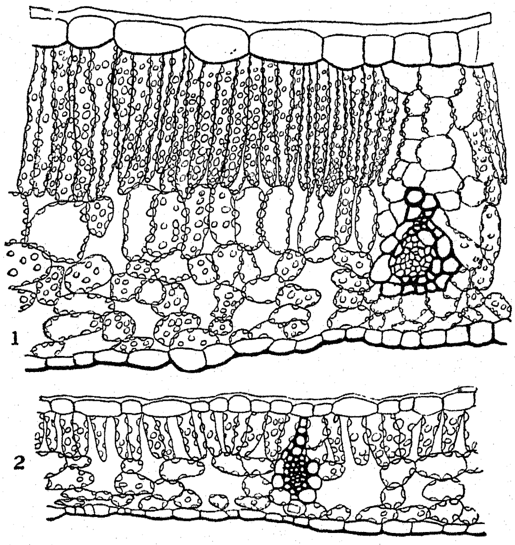

FIG. 164.—Leaves from (1) the south periphery and (2) center of the crown of an isolated sugar maple (*Acer saccharum*). (*After Hanson.*)

in the lower part. Some plants have their leaves "edge on" to the noonday sun. In these so-called *compass plants*, such as prickly lettuce

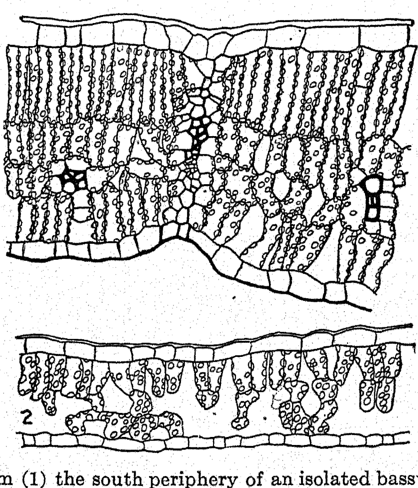

FIG. 165.—Leaves from (1) the south periphery of an isolated basswood (*Tilia americana*), and (2) from the base of a tree of the same species growing in a forest. (*After Hanson.*)

(*Lactuca scariola*), rosin weed (*Silphium laciniatum*), etc., the two sides of the leaf are equally illuminated and palisade develops more or less equally on both (Figs. 162 and 163). Conversely, in plants like the

mullein (*Verbascum*) where the chlorenchyma is screened from intense light by a dense growth of hairs, palisade tissue is poorly developed. In deep shade there is little or no difference in the intensity of the light received by the two surfaces, at least it is too weak to develop palisade, and shade leaves are often composed of a uniform chlorenchyma of sponge throughout.

The amount of palisade development in the same plant may vary greatly. The leaves of a tree that are fully exposed to the sun are very different from those of the shaded interior of the crown[213] (Figs. 164 and 165). In many cases, the transpiration rate from equal surfaces of the sun leaf and shade leaf is in the ratio of about 10:1. Palisade tissue is correlated with the development of chloroplasts as is indicated by the absence of palisading in albescent leaves. In many cases, it is discontinued sharply with failure of chlorophyll development. Finally, there are many instances, especially among monocotyledons, where palisade is never developed, and in some dicotyledons it seems to form without regard to external factors.

Changes in Form of Leaves.—The form of the leaf is largely determined by the action of light upon the chloroplasts and the consequent change in the form of the cells that contain them. Owing to the direction in which they elongate, sponge cells tend to produce an extension of the leaf at right angles to the light rays, while palisade cells extend the leaf in line with them. Hence, leaves that contain an excess of sponge tissue are relatively broader, while those in which the palisade is preponderant are relatively thicker. Since plants, so far as possible, economize material and energy, the broadened leaf tends to be thin, and the thickened leaf to be narrow. Hence, in general, sun leaves, which are produced in a relatively xeric habitat, are smaller and thicker than shade leaves grown in a mesic environment. This holds true not only for sun and shade forms of the same species but also for sun and shade plants generally. Similar differentiations occur in leaves of the same tree, shrub, or herb with a dense crown of leaves. Change in thickness may, more over, be brought about by modifying the water content of soil without change in the intensity of light.[476,515,540]

The outline of shade leaves is more nearly entire than that of similar leaves grown in strong insolation. Although this is not absolute, it may usually be shown by comparing the sun and shade forms of a species with lobed or divided leaves. There appears to be a clear correlation between lobing of leaves and rate of water supply and loss from the plant, but more experimental work is needed.

The stems of plants grown in shade are regularly taller and often more branched than corresponding sun forms (Fig. 166). It is clear that upon a stem with elongated internodes the leaves interfere less with the illumination of those below them. This is also true of the

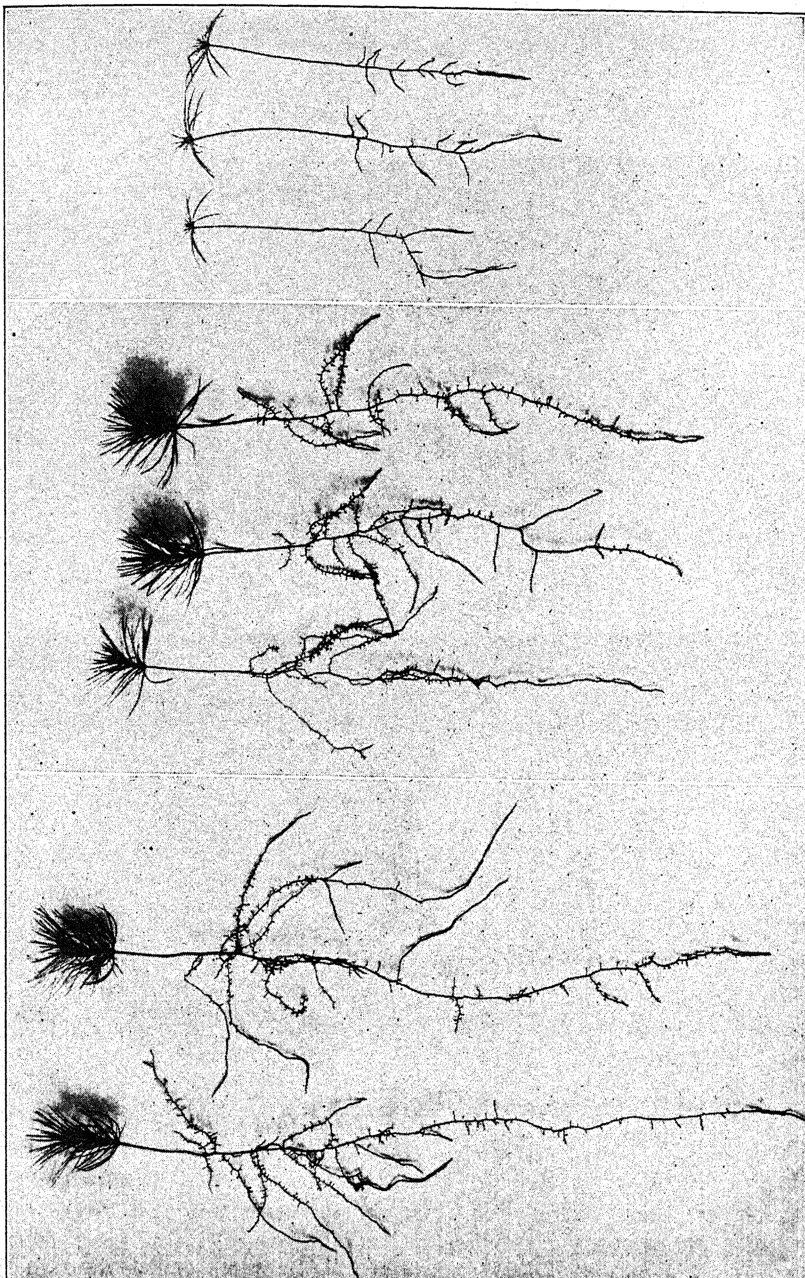

Fig. 166.—Seedlings of white pine of the same age grown in full light (left), half shade, and deep shade. (*After Burns.*)

branches, which serve further to carry the leaves away from the stem and from each other in such a way that the plant obtains the greatest possible exposure of its leaf surface.

Relation to Stomatal Movement.—Light is the most important environmental factor modifying stomatal movement. In nearly all plants, stomatal opening is correlated with the presence of light when other conditions for opening are favorable (Fig. 167). When they

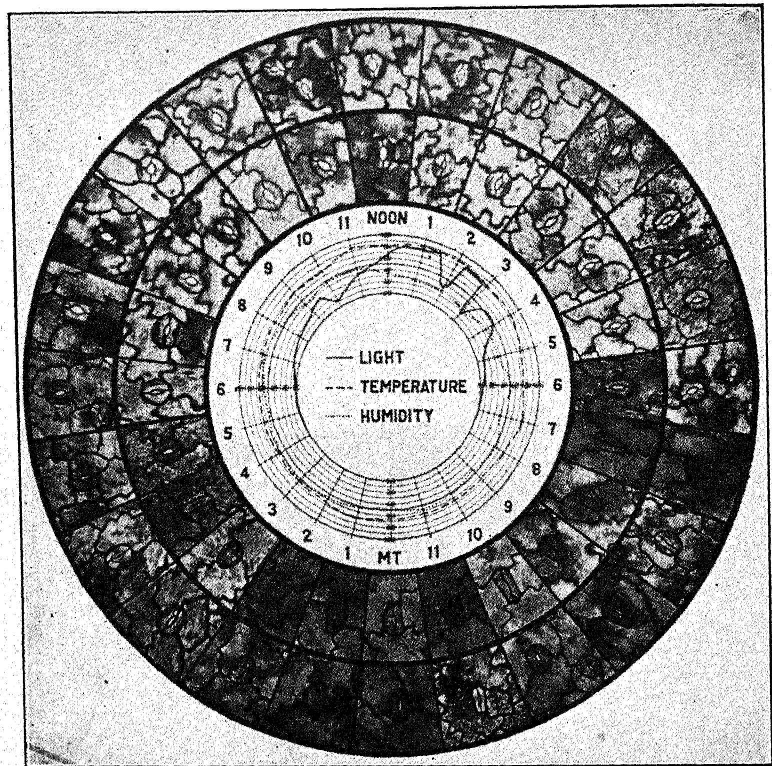

FIG. 167.—Stomata from the upper (outer circle) and lower epidermis of heavily irrigated alfalfa, and environmental factors during a 24-hour day. The figure consists of 48 separate microphotographs. (*After Loftfield.*)

become unfavorable, however, the influence of light is modified by the action of other factors and finally nullified. In a few plants, light seems to have little or no part in producing stomatal opening.[320]

The amount of water in the leaves and the acidity of the guard cells are the two internal conditions directly concerned with stomatal movement.[445] Under normal conditions, the sap of the guard cells is more acid when the stomata are closed. The cause of the increased acidity is not certainly known. It may be due to the accumulation of organic acids in darkness which are oxidized to carbon dioxide and water in the presence

of light or it may be caused by the accumulation of carbon dioxide resulting from respiration. This accumulation does not occur in light, since the carbon dioxide is used in photosynthesis, and hence, light decreases the acidity of the guard cells.[447] This makes conditions more favorable for greater hydration of the hydrophilous colloids of these cells as well as for the hydrolytic action of diastase. The increased intake of water by the guard cells results in greater turgidity and tends toward stomatal opening.[257,587] At the same time that the starch is changed to sugar, osmotic pressure is greatly increased, and the stomata open. A reversal of the process, *i.e.* increased acidity, appearance of starch, and decrease in turgor, occurs when the stomata close. The starch content of the guard cells may never wholly disappear, but usually it is lowest about 10 a.m. It rapidly increases during closure (Fig. 168). The rapid initial response of increased turgidity when light acts upon the guard cells is probably to be ascribed to colloidal hydration, while hydrolysis of carbohydrates seems to be a slower but probably more powerful reinforcement.[447]

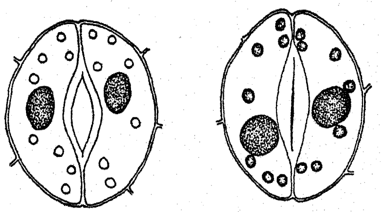

FIG. 168.—Stomata from lower epidermis of a cocklebur (*Xanthium commune*). Note the absence of starch in the chloroplasts in the open (day) condition and its abundance at night when the stoma is closed.

Other Effects of Light.—In the effects of light thus far enumerated, the stimulus is exerted primarily upon the chloroplasts. This is probably also the case in turning of stems and leaves and in the day and night position of leaves. It is impossible, however, as yet to establish this connection directly. The reaction does not appear in the chloroplasts or the cells containing them, but the stimulus is transferred to a more remote part of the plant (usually the petiole) where it becomes evident. Since such movements are largely confined to green plants and apparently result in placing the leaves in more favorable positions, it seems extremely probable that they are due, in the first place, to the effect of light on the chloroplasts. The effect of light on vegetative development and reproduction is discussed under duration of light.

EXPOSURE OF LEAVES TO LIGHT

Through long periods of evolution plants have become so molded in form and in structure as to bring the photosynthetic organs into advantageous relation with the controlling factor, light. The latter occurs rather equally distributed in all directions; hence, the aerial plant parts are usually radially symmetrical. Since light is of such a nature that it can not be transmitted far into the plant, the latter has become adapted by profuse and slender branching and ultimately by flattening and expanding the termini into the structures called leaves. In proportion

to the amount of structural material involved, coniferous trees with a broad base and progressively shorter branches upward, diverging from the excurrent trunk, approach the ideal for maximum illumination. Leaf arrangement resulting from such branching has been likened to a series of meadows, one superimposed upon the other without the interference of shading (Fig. 169). Upon the periphery of this framework the photosynthetic organs are displayed (Fig. 170). The almost hemispheric crown of the deliquescent trunk of an isolated elm or maple is similarly advantageous as regards leaf exposure to light.

FIG. 169 —Blue spruce (*Picea pungens*), note the arrangement of the branches in layers.

Many species have developed special methods of securing the display of their foliage in the light without the expenditure of sufficient materials to hold them erect.[118] Among such climbers are those which ascend merely by leaning against other plants (*e.g.* a nightshade, *Solanum dulcamara*); those which climb by hooks and thorns (*e.g.* the bedstraw, *Galium*, and various brambles); root and tendril climbers such as Virginia creeper and English ivy; as well as the more specialized group of twining plants. Since climbers are most abundant in forests, and especially in dense tropical ones, but few in open grassland or desert, it seems that this habit must have resulted from the struggle for light.

The exposure to light has been obtained with little expenditure of materials for stems.[592] A grapevine, for example, with a diameter of stem of only a few centimeters may have a foliage area quite as great as that of the tree which upholds it, although the latter has a trunk several inches thick. The structure of the stem is so modified as to be given over largely to conduction, as may be easily demonstrated (Fig. 171).

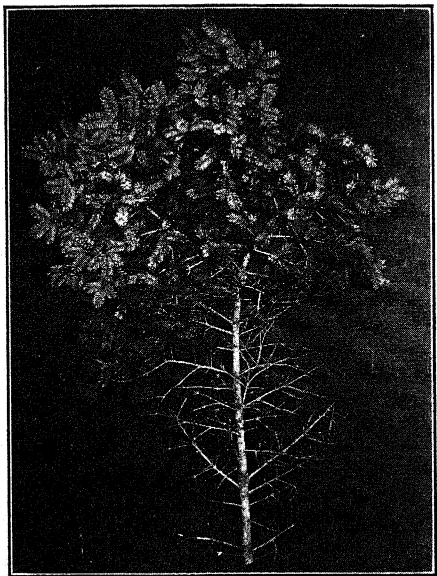

FIG. 170.

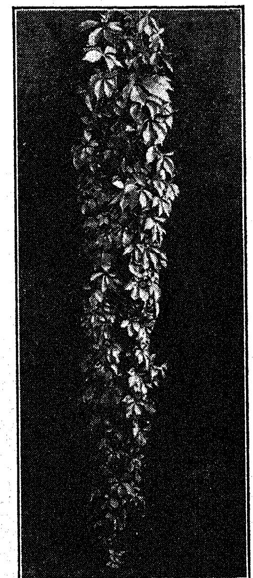

FIG. 171.

FIG. 170.—Branch of blue spruce showing typical loss of leaves near center of crown due to decreased light. This occurs although water content of soil is optimum.

FIG. 171.—Virginia creeper or woodbine (*Parthenocissus quinquefolia*) about 7 feet long. The total transpiring surface of 23 square feet was supplied with water through six small stems, averaging only 3.5 millimeters in diameter.

To Compare the Rate of Water Conduction in Climbing and Non-climbing Plants. Select stems of some woody vine such as grape (*Vitis*) or Virginia creeper (*Parthenocissus*) 6 to 10 millimeters thick, and cut a section 8 to 10 centimeters long. Select and cut branches of maple or oak or other tree of the same diameter and length, avoiding the nodes if possible. The sections should be cut under water or immediately placed in water. Procure rubber tubing that will fit closely over the stems. Fill a long piece of the tubing with water, siphoning it from a 2-liter container placed 10 feet above the worktable. While the tubing is filled with water, fasten it securely over one end of the stem and collect in a graduate the water that is conducted by the stem. Connect the second stem to another tube in a similar manner and determine the relative conducting power of the tree and climber for a period of 10 to 30 minutes. Examine the stems closely and suggest an explanation of the differences noted.

Foliage display in grasses and many other monocotyledons (*e.g.* sedges, rushes, iris, cattails) is of a distinctly different but scarcely less efficient type. Here the leaves develop in such positions that they cast

relatively little shade, and light is permitted to penetrate nearly or quite to their bases. At some time of the day, except in extremely dense growths, all of the leaves receive direct sunlight, and the total surface can be utilized in the manufacture of food. The advantage afforded by such an arrangement, together with the rhizome habit, goes far toward accounting for the dominance of grasses and grass-like plants in the treeless portions of the world.

Many intermediate forms abound. The foliage of many plants is arranged in a mosaic, *i.e.* the leaves are fitted together like the stones in a mosaic and in such a manner that each leaf is exposed to the most possible light. Plants such as dandelion, mullein, plantain, and evening primrose form rosettes near the soil. In these, each leaf is arranged so that it fills a space in the circle, and overlapping is reduced to a minimum. Where one leaf does overlap another, photosynthetic activity in the shaded portion of the latter is greatly reduced, in the case of the dandelion often 50 per cent.[321] The positions of leaves in response to light are very diverse, as may be seen almost anywhere. Epiphytes have solved the light problem by perching high upon other plants.[387] In some cases, they are so abundant as to cause considerable injury by shading the plant affording the support. In the same way, epiphylls, such as various species of lichens, characteristic of the moist tropics, are very injurious to the leaves on which they occur. In coniferous forests, the needles of the trees are sometimes shaded and even killed by the pendant growths of various lichens such as *Usnea*, *Alectoria*, etc.

RECEPTION AND ABSORPTION OF LIGHT

Plants possess no special structures for the reception of light. The radiant energy impinges upon all of the aerial parts, the characteristic form of the leaf being chiefly to increase the surface for absorption of both light and carbon dioxide. The general effect of the epidermis is to reduce the amount of light that enters the leaf, due partly to reflection and partly to absorption. The amount of light reflected depends upon the color, texture, and quality of the surface.

Dark green leaves like those of the lilac reflect less light than paler green ones such as the white poplar. Reflection from the white, hairy under surface of the leaves of the latter is sometimes 50 per cent of the incident light.[490] Leaves with a smooth or shining cuticle reflect much light. A thick cuticle or a dense coating of hairs absorbs much of the light that is not reflected. In some cases, *e.g.* wild ginger (*Asarum caudatum*), which grows in dense shade, the outer wall of the epidermal cells is convex. Thus, the light passing through the cuticle is more or less concentrated before it reaches the chlorenchyma. Similarly, in certain moss protonema growing in the weak light of caves, the convex outer surface of the cells concentrates the light on the chloroplasts

aggregated near the base of the cell. Such cases, however, are of rare occurrence and of little importance.

The light that enters the leaf must pass through the colorless epidermis and is then absorbed by the chlorenchyma. In submerged hydrophytes, epidermal chlorophyll usually occurs in abundance, but among terrestrial plants, chloroplasts in the epidermis are rare even in those species growing in dense shade, with the exception of ferns. Some light passes entirely through the leaf, but ordinarily this is slight. Thick or fleshy leaves absorb practically all the light that enters them. Thin leaves placed in sunshine transmit considerable light, but plants with such leaves are usually confined to shady habitats, where the light is very diffuse and the absorption relatively complete. Some idea of the amount of light actually used by the leaf may be obtained by determining the amount that passes through the epidermis and deducting from this that which passes through the entire leaf.

To Determine the Relative Amount of Light Absorbed by Various Leaves.— Select representative sun and shade leaves of a tree or shrub and of herbs grown in full light and dense shade. Variegated leaves of geranium, ribbon grass (*Phalaris*), or *Abutilon*, and others with prominent veining such as kidney bean (*Phaseolus vulgaris*), etc., should also be used. Place one leaf of each on the glass of an 8- by 10-inch printing frame, cover with a sheet of printing-out paper such as "solio," and fasten the back of the frame in place. Expose to the sunlight for 10 to 30 minutes until the paper about the leaves is thoroughly blackened and the network of veins shows very plainly. Remove the leaves and compare the relative darkening of the paper (*i.e.* penetration of rays chemically active on the sensitized paper) under the different leaves. Hold the leaf to the light and explain why the veins are printed so clearly. Make a list of the leaves in order of their absorption of light rays. The leaf prints may be kept permanently by "fixing" them for 5 minutes in a bath containing 150 grams of sodium hyposulphite dissolved in 500 cubic centimeters of water. The prints should be washed in water before drying.

NATURE OF THE LIGHT STIMULUS

The stimulus of light is exerted upon plants by a change in its quality, direction, intensity, or duration. In nature, the *quality of light* on clear days is apparently very little if any different in various habitats. Even in dense forests, it seems almost certain that the diffuse light is white, not green, although final solution of this question is still wanting.[91] Light reaches the forest floor by filtering through or between the crowns of trees or by reflection from the leaves and twigs and not by passing through the leaves. The amount of light passing unabsorbed through leaves is small, 0.03 to 0.6 per cent for sun leaves and 0.3 to 2 per cent for shade leaves.[65] A simple experiment shows that the thickness of one leaf is often enough to screen the light so completely that photosynthesis in the leaf below is entirely inhibited.

The quality of the light is modified by clouds, fogs, etc. The short wave lengths are most readily absorbed by the atmosphere and

especially when it is laden with moisture. Although ultra-violet light is invisible to the human eye, it produces certain effects upon plants. It is extremely harmful to bacteria, often causing their death and, with the short violet rays, has a retarding effect upon vegetative development. Since the longer wave lengths of the red end of the spectrum, which are most important in photosynthesis, are less readily absorbed, the quality of the light during cloudy days is somewhat different from that during clear weather. It seems possible that the difference of vegetative growth at low and high altitudes and in clear and foggy climates is partly due to differences in the quality of the light.

The *direction of the light* is of little importance except where the illumination is strongly one sided. The radially symmetrical development of a tree or other isolated plant shows clearly that strong diffuse (north) light is sufficient for normal development. Only plants on the edge of forests, thickets, etc., are often bent toward the source of light. Within the mass of vegetation such movements are lacking except in a few plants such as the mallow (*Malva rotundifolia*), cotton (*Gossypium*), and sunflower (*Helianthus*). These species have leaves that are so sensitive to light that the leaf blades are turned at right angles to the sun's rays in the morning, and by a gradual shift in position they follow the sun through its course, facing westward in the evening. By an orientation of the flower stalk, the sunflower head often behaves similarly.

The *change in light intensity* necessary to produce a response varies for different species, and it is also influenced by the intensity in which the species normally grows. The normal extremes are full sunshine, represented by 1, and a diffuseness of 0.002, *i.e.* light only one five-hundredth that of sunlight. Photosynthesis is so completely dependent upon light that it is affected by very slight differences of intensity. On the contrary, such responses as the movement of chloroplasts, changes in leaf structure, etc., are produced only by much greater differences.

The *duration of light, i.e.* length of day, exerts such profound effects upon the rate of development, flowering, and fruiting and upon the distribution of plants that it will be separately considered.

MEASUREMENT OF LIGHT INTENSITY

The measurement of light intensity is not a simple process and it becomes increasingly difficult where it must be made in the field and often in a small space among plants. No photometer that is entirely satisfactory has yet been devised. Ideally, both quality and intensity of the light should be determined for different hours of the day and for different days of the growing season in various habitats. A very useful instrument for measuring approximate differences in intensity in different habitats is the simple photometer.[45] It has been very extensively employed. In principle, it is based upon the fact that the darkening of

sensitized photographic paper is proportional to the product of the light intensity and the time of exposure. By this method, only the rays chemically active on the sensitized paper (*i.e.* the blue end of the spectrum) are measured, and it is assumed that the intensities of the others vary in proportion.

The instrument consists of a tight metal box containing a central disk upon which a strip of photographic paper is fastened in a groove (Fig. 172). The disk is revolved past an opening 6 millimeters square, which is closed by means of a spring that operates a slide working between two flanges. It is graduated into 25 parts that are numbered. A line just beneath the opening coincides with the successive lines on the disk and indicates the number of the exposure. The proper movement of the wheel for each successive exposure is indicated by a click. The metal case is made of two parts which fit together in such a manner that the bottom can readily be removed and the paper placed in position. The paper used is a slow printing-out paper such as solio. Strips 6 millimeters wide are cut lengthwise on a straightedge from 8- by 10-inch sheets with the emulsion side up. The paper is placed in the groove on the disk with the ends inserted downward through the small opening. It is best to crease the ends of the paper so that it will fit tightly before inserting the cork plug, which holds it in position. Great care should be exercised not to touch the emulsion side of the paper which is turned outward on the disk. When the paper is securely fastened in position, the cover is inserted and held in place by the thumbscrew on the side. The cover should be revolved until the 6-millimeter opening in it is just opposite the number 1 on the disk. A recent model of the stop-watch photometer is of vest-pocket size and all the operations are automatically made by pressing a plunger.

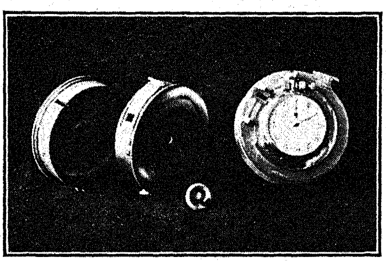

FIG. 172.—Simple photometers. The one on the right has a stop watch attached.

Making a Standard.—The photometer is held in one hand with the slit directed toward the noonday sun. A watch with a large second hand is held with it, thus leaving the other hand free to operate the shutter. An exposure is made by quickly withdrawing the slide in such a way as to uncover the entire opening, at the same time keeping the eyes fixed on the watch. The closure is made automatically simply by releasing the shutter. After a little practice, it is easy to expose the paper for the exact time desired. After each exposure the dial should be immediately turned to the next number.

The standard is obtained by making successive exposures 1, 2, 3, etc., to 8 seconds in length in full sunshine at noon on a clear day. Great care

should be exercised to make the time of exposure exact. It is desirable to make a second series to serve as a check upon the first. The standard is then removed in a dark room and placed in a light-tight box, such as is used for photographic films or plates. It should be used only in weak, electric light. When kept in a cool place and handled carefully, the standard and solio strips may be kept several weeks without appreciable change. It is best, however, to make a new standard from time to time during the growing season to serve as check upon the original.

Making Readings.—The best practice in making readings is to secure a decided tint that falls between the extremes of the standard. It is practically impossible to obtain a sunshine equivalent for very faint tints and equally difficult to match the very deep ones obtained by long exposure. Consequently, the most satisfactory method is to expose until a good tint is secured but one that is not deeper than the 5-second tint of the standard. In deep shade, this often requires several minutes, and in such places it is usually more satisfactory to stop the exposure with the lighter tint, approximating the 1- or 2-second exposure of the standard. The stop-watch photometer, which differs in having a stop watch which automatically indicates the time of the exposure, is somewhat more convenient and increases the accuracy of the reading. In taking readings, the date, time of day, place of reading, number of instrument and of exposure, and the time of the exposure in seconds must be carefully recorded. As a rule, readings are made only on clear days, except where the light values of cloudy days are desired for special purposes. After a strip has been completely exposed, it is removed in the dark, and a new one is put in place. In removing the strip, the number of each exposure should be marked on the reverse side of the paper.

Comparison with the Standard.—The light intensity denoted by each exposure is ascertained by comparing it with the standard. It is best to cut off the part of the strip on which the first reading was made and hold it with tweezers while comparing with the standard until the tint that matches is secured. With a little practice, this may be readily done. Skill and certainty in making the tints match are obtained by comparing the exposed strip with the standard a second time. If this is done without reference to the first results, the two comparisons serve as a valuable check upon each other. Proceeding in this manner, all of the readings are matched with the standard. Interpolations between colors may be made, if desirable, when the proper match is secured for a particular exposure. The comparative light intensity is found by dividing the duration of exposure in seconds by the duration for the standard tint. Thus, if an exposure in shade for 100 seconds matches a 2-second standard, the light is fifty times more diffuse or weaker than the sunlight. The latter is taken as unity, and the light intensity in the shade is $2 \div 100 = 0.02$, *i.e.* 2 per cent.

Measuring Light Intensity.—Make a series of light readings in the several habitats where other factors are being measured. It is best to make three readings, using different lengths of time of exposure in each place, and average the results. In forest, scrub, etc., where the light is not uniform, move the photometer slowly back and forth during the exposure, keeping the opening directed toward the sun, in order to secure an average of the light intensities. Are the light values the same at different levels in grassland, scrub, and forest? Give reasons for your conclusions. Compare that of the interior of the crown of a tree with the light received by the leaves on the north and south periphery. Also determine light intensities in the greenhouse and on cloudy days. The photometer may likewise be used to determine the amount of light that penetrates through various leaves by holding the leaf closely over the slot during the exposure.

CAUSES OF VARIATION IN LIGHT INTENSITY

The primary object of light readings is to determine the amount of light in various habitats or partial habitats, as a basis for explaining the differences shown by the plants themselves. In striving to measure such differences, it is absolutely necessary to avoid errors arising from the condition of the weather, time of day or year, latitude, altitude, and slope.

Even very fleecy clouds in front of the sun result in appreciable reduction of light, and the light is greatly reduced by heavy clouds and fogs. In certain oceanic climates, heavy fogs are so prevalent and the light is reduced so regularly that it may become a limiting factor to photosynthesis and growth. In northern latitudes, such as Alaska, where rainfall is abundant but the temperature too low for the best development of vegetation, the amount of sunshine becomes an exceedingly important climatic factor. Light readings should be taken only on clear days.

Both intensity and quality of light are markedly reduced by a layer of water, and submerged plants grow under an illumination quite different from that of terrestrial ones. The fact that bodies of water are blue or greenish blue indicates that the other rays of light are absorbed and only those of short wave length are reflected, or transmitted to any considerable depth. When the surface of the water is smooth, 20 to 25 per cent of the light may be reflected, and in rough water this may be increased to 50 or even 70 per cent. In the ocean, even light of short wave lengths may be reduced under the most favorable conditions to approximately 10 per cent at a depth of 10 meters.[173] The red pigment, phycoerythrin, of the red algæ (*Rhodophyceæ*) is complementary to the blue light rays and because of this the plants of the deep water are able to absorb the latter much more advantageously.[514]

Effect of Time.—The intensity of the light varies throughout the day and the year. Except where plants are considerably shaded, when the sky is clear it is only for a short time near sunrise and sunset that light is a limiting factor to photosynthesis. The daily maximum occurs at noon "sun time," a point which itself moves back and forth through the year. The daily minimum is reached at nightfall, and it lasts until

dawn. The annual maximum falls on June 22, the minimum upon Dec. 22. The greatest light intensity occurs when the sun is at its highest altitude, *i.e.* when the angle that it makes with the surface of the earth is greatest, and lowest when this angle is least. The effect of angle upon light intensity is due to the absorption of the light rays by the atmosphere. This absorption is greatest near the horizon, where the pathway of the rays is longest, and it is least at the zenith. In other words, the absorption is greatest at sunrise and sunset, least at noonday; greatest in December and least in June.

During the growing period of 6 months, beginning Mar. 21 and closing Sept. 23, the highest and lowest noon intensities are 0.98 and 0.93, respectively, at the latitude of Lincoln, Nebraska. Between 9 a.m. and 3 p.m. during this period, the range would be from 0.82 to 0.98, a difference that is practically negligible. Hence, in all ordinary study, the value of readings taken in full sunlight between 9 a.m. and 3 p.m., Mar. 21 to Sept. 22, may be regarded as unity. Consequently, readings made in shady habitats during the same period may be compared with them directly without making allowance for the slight error. Naturally, when readings are taken simultaneously, no error exists, and the same is practically true of readings made between 10 a.m. and 2 p.m.

Effect of Altitude and Slope.—Altitude affects the amount of light by decreasing the distance that the rays must travel through the atmosphere, thus decreasing absorption. It is estimated that 20 per cent of a light ray is absorbed before it reaches sea level. At the top of Pike's Peak (altitude 14,100 feet), the absorption is 11 per cent. In the one case, the light is 80 per cent of that which enters the atmosphere; in the other, 89 per cent. The difference in intensity between them is altogether too small to have any important effect on photosynthesis.

The amount of light received by a south-facing slope is greater than that received by a level area, and that striking a north-facing slope is least. Except that the duration of light on the south slope is longest, the difference is of little significance. Leaf position as regards incident light is the same in all cases. The vegetation on north-facing slopes of steep mountains and valleys in north temperate regions may receive little or no direct sunlight. The sharp difference in the type of vegetation as compared with fully insolated slopes is due to differences in temperature and water relations of soil and air. There is abundant light for photosynthesis, although it is diffuse light in the former community.

INFLUENCE OF DECREASED LIGHT INTENSITY

All green plants require light, although bacteria and fungi may flourish even in dark caverns and in the depths of the ocean. In fact, many species of saprophytic plants are killed by exposure to light, a fact clearly recognized in sanitation. Many saprophytic and parasitic fungi

that can grow vegetatively in the dark require light for reproduction. Most plants utilize only a very small part of the light received. The minimum amount required varies with the species and stage of development and is also greatly influenced by other factors of the environment. The optimum amount for many species is less than full sunshine; some plants make their best development in light of low intensity. Thus, the seedlings of Douglas fir thrive best at about 50 per cent of full sunshine.

Reduction in light intensity tends to increase the length of the main axis and its branches and to promote the growth of broad, thin leaves with loose, open structure. The total absence of light results in greatly attenuated, weak stems with little mechanical tissue, few or no branches, and leaves often reduced to mere scales that usually lack palisade tissue. The moisture relation probably also plays a part in this morphological response. The plant is pale yellowish or whitish in color, due to lack of chlorophyll, and is said to be etiolated. The largest leaves and fullest development of many plants occur in partial shade.

Effect of Light Intensity on Form and Structure of Plants.—Construct in the greenhouse a series of two or three shade tents 1 meter square and high. The framework of wooden strips, ¼ by 1 inch, may be nailed to a table or greenhouse bench and the cloth fastened to it by means of thumb tacks. Light intensities of approximately 10, 5, and 1 per cent may be obtained by using coverings of white cheesecloth, muslin, and double thickness of black cambric, respectively. The tent should be so constructed that the lower half of one side may be easily opened. Ordinarily, the humidity may be controlled by the amount of watering, but if it becomes too high, a hood for ventilation should be arranged at the top or sides.

Practically all flowering plants will show some adaptation to the different light intensities, although some are much more plastic than others. Start seedlings of various species in ordinary greenhouse light, *e.g.* sunflower, four-o'clock (*Allionia*), dandelion, shepherd's-purse (*Bursa*), bedstraw (*Galium*), evening primrose (*Œnothera*), etc. Then place two of each species in each tent and keep two for controls. Water as necessary; the weaker plants in deep shade will require but little.

During the growth of the plants, make occasional readings of the light intensity and humidity for the several tents and that of the greenhouse outside. Also, make one determination of the starch content of a representative leaf of each species for each habitat. Follow from week to week the effect of shade upon leaf size and outline and form of the rosette in dandelion; note the stretching of the petioles and internodes in *Bursa* and *Œnothera*, and observe other differences in growth and behavior. When the plants are well grown, make an outline drawing or photograph of one series of four plants, all to the same scale. Select a representative leaf from each form, and make a leaf print for the four forms of each species. Cut cross-sections of the leaves of one series and make out the differences in total thickness, development of palisade, sponge, thickness of cuticle, etc. Prepare a concise account of the adaptation of one of the species concerned to different light intensities, explaining, in so far as possible, the changes observed.

Partial shade increases succulence and delicacy of structure. Many vegetables such as asparagus, cauliflower, celery, and lettuce do best under such conditions. Half-shade is employed in forcing rhubarb, and in pineapple culture, especially in Florida. Tea is grown in the shade of

taller trees often planted in alternate rows, since under these conditions the leaves attain their best quality and yield. Coffee is likewise produced most profitably in subtropical regions when partially shaded by forest trees. Ginseng, which normally grows in woodland shade, is protected from full sunshine when grown commercially by frames made of slats. Partial shade produces large, broad, thin leaves with poorly developed veins and relatively large air spaces and an abundance of sponge parenchyma, as is shown by the growth of tobacco for cigar wrappers under conditions of half-shade.[583] It must be constantly kept in mind, however, that reducing the light also has a marked effect upon other factors, especially soil moisture, humidity, and temperature. In forest nurseries and elsewhere, lath shelters are widely used to maintain the proper conditions for seed beds of many kinds of trees.

While diffuse light promotes the development of vegetative structures, intense light favors the development of flowers, fruits, and seeds. The great profusion of flowers in grassland throughout the growing season is largely due to the strong light. In deciduous forests, flowers are abundant only before the new leaves of the forest canopy are developed; in dense coniferous forests, flowers are never abundant. The greatest profusion of brightly colored flowers is found in alpine meadows where the light is very intense.

Many crops grown for their vegetative parts, such as potatoes, carrots, turnips, and garden beets, yield best where there is a high percentage of cloudy days. Conversely, the greatest grain-producing areas are in regions where there is a high percentage of bright, sunny days. Such are the grasslands of the central United States and of eastern Washington. Fruit is likewise produced in great quantities where the light intensity is but slightly reduced by clouds or atmospheric moisture during the entire growing season and often under irrigation, especially in California, Washington, and Colorado. The yield of cotton fiber and seed is greatly reduced throughout the cotton belt, during unusually cloudy, wet years, although the plants make an excessive vegetative growth.

TOLERANCE

Tolerance is largely the ability of a plant to endure shading. Seedlings of hard maple, beech, linden, spruce, and hemlock are all very tolerant of shade. But those of light-demanding trees such as willow, cottonwood, and lodgepole pine are intolerant. Similarly, many shrubs and herbs such as sumac, bluestem grasses, and sunflowers are light demanding, while the spicebush and bloodroot grow in deep shade. It is because of the adjustment of certain types of vegetation to decreased light intensity that layering occurs. Layers may be seen in various plant communities such as reed swamps, grassland, and scrub, but they are most pronounced in forests.

The number of layers is controlled mainly by the density of the forest canopy, although other factors such as water content often play an important part. In an open woodland, where much light filters through between the leaves and branches, layers of shrubs, tall herbs, low herbs, and a ground layer of mosses, lichens, liverworts, and fungi are usually more or less developed. But where the crowns of the trees grow closely, as in medial or climax stages of deciduous forests, because of decreased light, some of the layers and frequently all but the low herb and ground layers disappear. The herbs show their most vigorous development during spring and early summer before the leafing out of the trees still further reduces the light.[299] In such habitats, intolerant plants can not ecize. A tree to become established in a closed forest must function and grow as a seedling and sapling in very subdued light, although later in life it may take its place in the forest canopy and receive full sunshine. Hence, only those that are tolerant can ecize.

A knowledge of tolerance is especially important in forest management.[22] In fact, technical forestry or silviculture is largely based on the concept that the different species of the forest vary in their demands for light, *i.e.* their tolerance of shade.[24,26] The outcome of mixed plantations depends upon the difference in tolerance between species. Intolerant species will disappear, since they can not reproduce themselves in shade. Tolerance likewise determines the outcome of plantations made under the canopies of old trees that do not reproduce themselves. The methods of cutting or thinning are similarly determined, less valuable but tolerant species, such as hard maple, often being removed to promote the growth of less tolerant but more valuable ones, such as white pine, etc.[162] In the natural development of forests through the various successional stages, light is a controlling factor.

Trees may be grouped according to their ability to carry on photosynthesis and grow in decreased light intensities, *i.e.* according to their tolerance. The following sequence, however, is not absolute, the most tolerant being placed first:[606]

Broad-leaved Trees	Coniferous Trees
Very tolerant:	Very tolerant:
Sugar maple (*Acer saccharum*)	Yew (*Taxus*)
Beech (*Fagus*)	Spruce (*Picea*)
Linden (*Tilia*)	Hemlock (*Tsuga*
	Firs (*Abies*)
	Cedars (*Thuja*)
Tolerant:	Tolerant:
Elms (*Ulmus*)	White pine (*Pinus strobus*)
White oak (*Quercus alba*)	Douglas fir (*Pseudotsuga*)
Red oak (*Q. rubra*)	
Ash (*Fraxinus*)	
Black oak (*Q. velutina*)	

Broad-leaved Trees	Coniferous Trees
Intolerant:	Intolerant:
Soft maple (*Acer saccharinum*)	Yellow pine (*Pinus ponderosa*)
Bur oak (*Q. macrocarpa*)	Larch (*Larix*)
Birches (*Betula*)	Lodgepole pine (*Pinus contorta murrayana*)
Poplars (*Populus*)	
Willows (*Salix*)	

It may be noted, for example in the development of deciduous forest, that the species characteristic of medial and climax stages of succession are all tolerant.

FIG. 173.—A young forest of closely growing Douglas fir, tamarack, and white fir. Note the absence of branches due to low light intensity.

Methods of Determining Tolerance.—There areseveral methods of determining the relative tolerance of forest trees.[606] Empirical scales of tolerance may be prepared by studying such characters as density of crown, self-pruning, relative height-growth, and the growth of the young stand under the old. An examination of the interior of the crown of intolerant trees, *e.g.* soft maple or yellow pine, will show that nearly all of the leaves occur on a peripheral hollow shell where they are well illuminated. The crown is not dense. In the pine, the lower whorl of branches, clothed with needles only on their termini, extends outward in such a manner that the branches are only slightly shaded by those just above and these, in turn, only moderately so by those still higher. The leaves of intolerant trees can not make food in weak, diffuse light.

Conversely, the density of the crowns of hard maple and linden, for example, is much greater and the interior fairly well clothed with shade leaves.

In the forest, the lower leaves and branches of intolerant trees die and fall to the ground. Hence, the tree grows slender and straight, its height being very great in relation to its diameter. Tolerant species, such as *Thuja*, retain their branches, and the stem is thick in proportion to its height. The Indians found that certain spindling, close-growing, intolerant trees, upon the removal of the bushy tops, made a very desirable framework for their tepees, hence the name *lodgepole* pine (Fig. 173). Finally, a study of the growth of young trees under the parent trees throws much light upon their ability to endure shading. In mixed forests with a closed canopy, saplings of the bur oak may succumb under light intensities where those of elm, beech, and sugar maple will thrive.

Factors Affecting Tolerance.—In using these criteria of tolerance, it must be kept in mind that soil moisture may also play an important and often a controlling part. When photosynthetic activity is low, development of roots is decreased more than that of the aboveground parts. Consequently, a seedling with insufficient light is subjected to much greater danger from drought or lack of soil nutrients. A classical example is that of Fricke's experiment in Europe where isolated groups of 10-year-old Scotch pines were found growing among their 70- to 100-year-old parents. The younger generation was growing poorly, apparently because of deficient light due to the crowded condition. A ditch 10 inches deep was dug around a group in the spring, whereupon the new needles increased their growth to twice that of their neighbors and also that of the preceding year. An herbaceous flora, moreover, appeared beneath the pines, quite in contrast to that of adjacent, similar areas. In digging the trench, the widely spreading, superficial roots of the parent trees, which extended into the territory occupied by the younger generation, had been cut. The vigorous growth was thus a response to increased water content and not to increased light[168] (Fig. 174).

Tolerance also varies with soil fertility and such climatic factors as temperature. White pine, for example, can stand less shading in Maine than in the mountains of North Carolina. Norway maple can live under 2 per cent light in Vienna, but 20 per cent is required in northern Norway. Since by far the greater part of the radiant energy is transformed into heat, the reason for these facts seems clear.[606] In fact, in a study of tolerance, emphasis must be placed upon the physical effects of radiant energy. Many intolerant trees, such as yellow pine, rarely form close, dense stands. Hence, much of the thermal effect of the radiant energy is lost because of wind movement. Among tolerant trees of dense stands, such as spruce, there is little air movement, and consequently the total heating effect even of low illumination is high.[21]

Knowledge of light intensities under various forest canopies helps to explain the ability of different species to endure shade.[356] The minimum light for sustained growth of yellow-pine seedlings is about 25 per cent, for Douglas fir 5 per cent, but that for Engelmann spruce is only 2 per cent.[21] The minimum light at which photosynthesis occurs in western yellow pine has been found to be 17 per cent, but only 1.9 per cent is

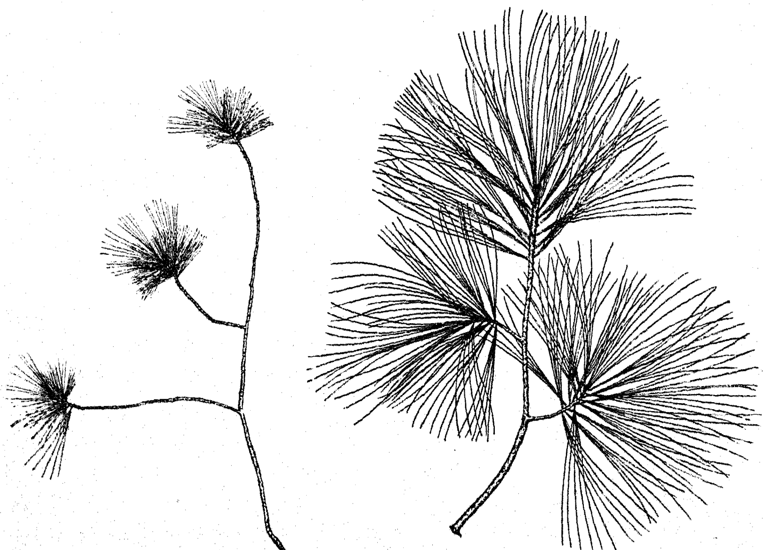

FIG. 174.—Normal development of needles of white pine (*Pinus strobus*) right, and their poor growth in the dense shade of tolerant, deciduous trees.

required for the very tolerant sugar maple.[67] The relative light intensities during midsummer in a mixed forest of black and bur oak and one of linden in Nebraska, where each species was reproducing its kind, respectively, were as follows:

	6 a.m.	8 a.m.	10 a.m.	12 M.	2 p.m.	4 p.m.	6 p.m.
Oak forest	5.3	5.5	20.0	20.0	20.0	11.6	10.0
Linden forest	1.8	2.0	6.6	10.0	4.6	4.3	2.5

In the oak forest, layering was pronounced; in the linden community, all but the ground layer had disappeared and no tree seedlings except those of the very tolerant linden were able to survive.

A Study of Tolerance.—From your field observations supplemented by use of the various methods of determining tolerance, make a list of the more important forest or shade trees of your region. Use one list for deciduous and one for evergreen species and subdivide each into very tolerant, tolerant, and intolerant species.

A determination of the relative tolerance of trees under conditions where all the factors, including the supply of light, can be controlled is desirable. Under an artificial, pure white light, where all other conditions were favorable, the minimum requirement for yellow pine was 17 per cent, Douglas fir 7.6, Engelmann spruce 5.9, white pine 5.8, hemlock 4.7, beech 4.2, and hard maple 1.9.[67]

A study of leaf structure gives much information about the tolerance of a species. Those that adapt themselves most completely to a variety of light conditions are naturally those which will survive best if placed under severe conditions as regards reduced light. This method, however, can give only relative comparisons, since the structures of leaves are variable even under the same conditions of light. As already pointed out, leaf structure is also profoundly affected by the water relation.

DURATION OF LIGHT

The duration of the light period in nature varies from 12 hours at the equator to continuous sunlight throughout the 24 hours during a part of the year at very high latitudes. Thus, tropical plants are exposed to intense light during half of each day while Arctic plants grow in weak light continuously or nearly so throughout the summer. The long summer days of high latitudes enable plants to develop rapidly and mature quickly. Photosynthesis is probably continuous under such conditions although lowest at midnight. Species transplanted from lower latitudes and grown under the continuous sunlight of northern Scandinavia for 2 months had the vegetative period considerably shortened.[454] It is largely due to the longer day, although, in part, to the protection afforded by the surrounding mountains from cool night winds, that oranges ripen earlier in the northern end of the Central Valley of California than 400 miles farther south.[378] Likewise, the continuous or long daily periods of sunshine during summer make it possible to produce bountiful crops of hay, potatoes, and other vegetables along the coast of Alaska. The potato, which is a cool-climate crop, gives enormous yields, owing to the long period of illumination, along the Mackenzie River at the Arctic Circle.

Effect of Length of Day.*—There is a marked tendency for plants of temperate climates to flower and fruit at only certain periods of the year. The yellow bell, redbud, crocus, violet, etc., blossom early in spring. As summer approaches, the iris, rhododendron, and poppy begin to bloom, while asters, dahlias, and chrysanthemums are characteristic of fall. These differences in time of reproduction are not related to temperature but to the daily duration of light and darkness. Even

* Materials for this section, exclusive of illustrations, have been almost entirely secured from the publications of Garner and Allard.[178,179,180,181]

though appropriate temperatures are provided out of the regular flowering and fruiting season, often the flowers and fruits fail to appear.

Violets kept in the light daily for a period corresponding to the daylight hours of spring, bloom at all seasons of the year. Similarly, chrysanthemums blossom in midsummer, provided they are given daily illumination of a duration equal to that of the late autumn days. If the short winter day is extended by means of electric illumination until midnight, iris will blossom in December, provided, of course, that the temperature, water, and nutrient relations are suitable. Ordinary

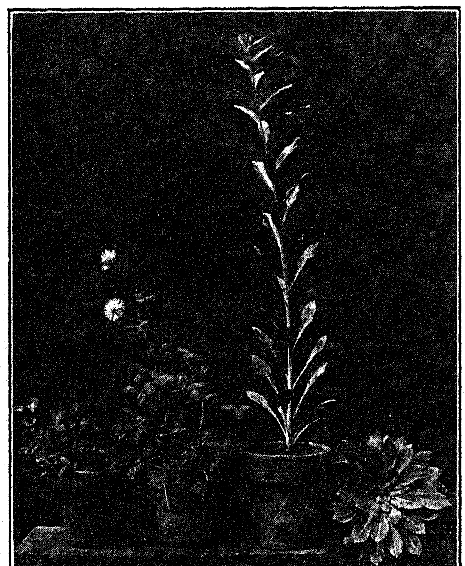

Fig. 175.—Long-day and short-day plants of red clover and evening primrose. One lot of the seedling clover and one rosette of *Oenothera* were grown six weeks under the short days of winter, and the others (center) were, in addition, illuminated until midnight.

40-watt, incandescent lights placed a few feet above the plants may be used. But even an average light intensity of about 4 candlepower at the surface of the soil is sufficient for bringing many plants into bloom, although, in some cases, higher illumination is more efficient[277] (Fig. 175).

A large number of species are more or less responsive to the daily light period.[1a] In many species, the action of the light period under ordinary circumstances is dominant, the response of the plant being prompt and certain under a rather wide range of environmental conditions. Some species and varieties respond to long days by flowering and fruiting, others to short ones. While, as a whole, there are sharp contrasts between the two groups, there are many species which apparently occupy an intermediate position.

Long-day and Short-day Plants.—Some plants require long days for successful flowering and fruiting, although they make a vigorous vegetative growth during short ones.[534] Typical examples are the radish, iris, red clover, the smaller cereals, evening primrose, and spinach. These flower regularly during the long days of late spring and early summer. All may be brought into blossom and fruitage in midwinter, however, if artificial light is used to prolong the daily illumination period to 15 or 16 hours.

Short-day plants such as beggar's-ticks (*Bidens*), tobacco, dahlia, ragweed, and cosmos continue to develop only vegetatively under a long-day illumination. They come into blossom normally only when short

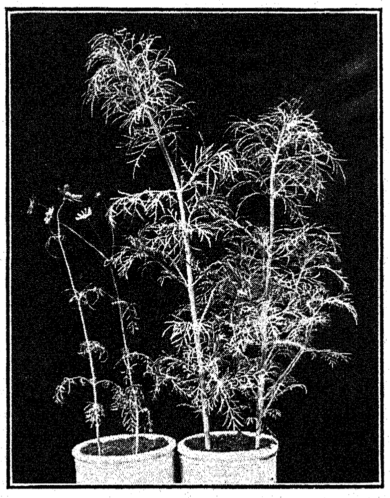

FIG. 176.—Cosmos about 60 days old. Those in blossom received light from 9 a.m. till 4 p.m. daily; the others throughout the long summer days of June at Lincoln, Nebraska They were placed in the small jars for photographing.

days occur. This is true of a large group of plants including most late-blooming summer annuals. Experimentally, they may be caused to flower in midsummer by excluding the early morning or late afternoon light for a few hours each day (Fig. 176). If, however, these plants are darkened for the same number of hours during the middle of the day, the vegetative period is not materially shortened. Cosmos under a short day, although dwarfed in stature, actually blossoms within 60 days after the germination of the seed, while under long-day illumination it continues growth and may attain a height of 15 feet.

Ever-bloomers.—This group occupies a position intermediate between the two preceding and shows some of the features of both. The cultivated sunflower, for example, is not materially influenced in time of flowering by the length of day, at least in medium-high latitudes, although the stature attained is greatly affected. While in temperate regions most

plants have a comparatively short period of flowering and fruiting each year, the length of time varying with the species, reproductive activity in some continues through several months. The latter are known as ever-bloomers or ever-bearers.

Near the equator, where the days are always 12 hours long, many plants have developed the ever-blooming or ever-bearing habit. Under natural conditions, the seasonal change in length of day in the United States is such that only a few plants show a pronounced type of ever-blooming. A number of common weeds such as chickweed (*Stellaria*) and dead nettle (*Lamium*) are of this class. These plants continue to grow and to flower in the field more or less persistently not only throughout the summer but also in the winter, if removed to the greenhouse. They are conspicuously different in their behavior from the majority of non-tropical plants which have their definite floral season. Several species of plants, however, when exposed to a length of day distinctly favorable to both growth and sexual reproduction, show a tendency to exhibit the "ever-blooming" or "ever-bearing" habit, *i.e.* the ability to continue both vegetative and reproductive activities more or less successfully together.

Many annual plants such as soy beans and ragweeds, when subjected to a particular length of day, complete two annual cycles as regards vegetative growth, flowering and fruiting within a period of about 4 months. The perennial aster behaves in a similar manner. Conversely, under certain light exposures, the vegetative development of annuals may be lengthened almost indefinitely, the plants behaving like non-flowering perennials. Thus, it may be that the cycle of alternating vegetative and reproductive activities as an annual event is due to the yearly periodicity in the length of day.

To Study the Development of Long- and Short-day Plants.—During the short days of late fall or winter, arrange a black curtain and overhead lighting in such a manner that one bench in the greenhouse may be artificially illuminated until midnight, while the rest of the greenhouse is in darkness. The curtain should be drawn aside by day so that temperature, humidity, and all other factors except length of the period of illumination are the same. Transplant into large pots, rosettes of evening primrose (*Œnothera biennis*), and rhizomes of iris that have been subjected to freezing temperatures. Also, grow seedlings of red clover, cosmos, Biloxi soy bean, ragweed (*Ambrosia*), or other long- and short-day plants 2 or 3 weeks before beginning the experiment. Select six of the best plants of each species and place three under long-day illumination and leave the other three under that of the short day. Examine and compare the development of each species once each week. The experiment should be continued at least 6 weeks or until the plants blossom.

Effect on Food Accumulation.—Plants also differ in the light period best suited to the production of reserve food supplies such as occur in tubers, bulbs, corms, and also resting buds. Such light periods do not correspond with those that promote shoot growth. Many plants

produce tubers or fleshy roots only under the influence of a comparatively short day. Such are the Irish potato, Jerusalem artichoke (*Helianthus tuberosus*), and yam. In all cases studied, typical tuber formation takes place as a result of decrease of the daily light below the optimum for stem elongation. Thus, tuberization is greatly favored by the shortening of the day in fall following the long summer days of high latitudes. Conversely, bulb formation, as illustrated by the onion, takes place as a result of increase in the daily light period above the optimum for stem growth.

Cause of Behavior.—In addition to influencing the fundamental process of photosynthesis, the duration of the daily light period may definitely control other parallel processes of fundamental importance in plant growth and development. It may determine not only the quantity of carbohydrate produced but also the utilization of this material. It is not possible, however, to explain the effect upon this basis alone. Growth relations and definite form of expression as controlled by length of day are regularly associated with characteristic acidity relations and probably with the water content of tissues. More work is necessary before the phenomena can be fully explained.

Effect on Distribution.—Plants that require a long day to flower and fruit obviously can not maintain themselves in the tropical zone even though increase in altitude may afford favorable temperatures. The existence of the more extreme types of short-day plants is likewise impossible. Passing from the equatorial regions into higher latitudes, temperatures promoting active vegetative growth are restricted to a summer period which, other conditions being equal, becomes progressively shorter as the polar regions are approached. The summers are characterized by lengthening periods of daylight and the winters by decreased length of day. Should plants like the ragweed, which requires about a 15-hour day to blossom, migrate northward, flowering would be progressively delayed later and later in the year until the days become sufficiently short. The seeds might freeze before maturing. If the plants were carried still farther north, they might not be able to blossom at all because of a too great length of day during the growing season. Hence, they could not ecize. Thus, any comprehensive study of the factors affecting the distribution of plants should take account of length of day along with the usual ones of temperature, water content, and light intensity.

Practical Significance.—Among field and garden crops, some plants are grown for their vegetative parts alone, others for their fruit or seed, and still in others maximum yields of both vegetative and reproductive parts are desired. A difference of 2 or more weeks in time of planting may definitely determine whether the plant activities will be directed toward the purely vegetative or the reproductive form of development.

These facts strongly emphasize the importance of accurately knowing the correct time for planting each crop in order to secure the highest returns. Even different varieties and strains of the same species differ markedly as to the particular length of day most favorable for flowering or for vegetative development.

Knowledge of *photoperiodism*, as these responses to length of day are called, should aid the plant breeder to secure for any particular region earlier or later varieties, more fruitful or larger growing forms, and improved ever-bloomers and ever-bearers. The problem of extending the northern or southern range of crop plants is also more clearly defined. Judgment as to the adaptability of species in a new region is, moreover, placed on a more adequate basis. Plant breeding should be greatly simplified and hastened through artificial control of light duration. Plants may be made to blossom at will at any time of the year, and crosses between parental types heretofore impossible, because of their flowering at different times of the year, accomplished. With proper knowledge of the specific requirements of each kind of plant, florists should be able to force flowering at any desired time during the year. The methods involved are simple and the results decisive.

CHAPTER XIV

PLANT RESPONSE AS A MEASURE OF ENVIRONMENT

Any attempt to determine exactly the causes which are producing modifications in the individual plant, and consequently in vegetation, must include careful measurements of all the factors of the habitat. These must be made with instruments of precision in order to ascertain the exact amount of each factor that is present. Measurement forms a basis for determining the ratio between the stimulus and the amount of functional and structural adjustment that results. A fundamental and apparently inevitable objection to all instruments, however, is their failure to express factor differences in terms of plant activities. While, moreover, instruments record the individual factors, most of them fail to integrate the various factors concerned. This is a serious drawback, since measurements of functions are regularly obtained as sums. Even with a complete set of measurements of habitat factors, the interpretation is difficult, for the amount or intensity of any factor necessary to produce a functional or structural response can be determined only by observing the response of the plant. Thus, while factor intensities must be measured by instruments, the effects that produce changes in vegetation must be determined by the living organism, the plant.

The *phytometer* (plant measure) is designed to express the physical factors of the habitat in terms of physiological activities.[95,388] It consists of plants grown, at least for a time, in the several habitats that are to be compared. Several plants are employed in each habitat so that variability of the individual is checked out.

Control Phytometers.—Phytometers are of many kinds, one of the simplest consisting of plants in sealed containers (Fig. 177). Since the factors of the soil may be varied at will, these are termed control phytometers. The containers are filled with fertile soil of good water content, in which the seeds are planted, and covered with a sand mulch until the seedlings have appeared. An optimum water content is maintained by watering from time to time in amounts just sufficient to bring the container back to its original weight. For long-time experiments, provision is also made for aeration by means of a tube (automobile-tire stem) with threaded end, soldered to the bottom of the container and to which an exhaust pump may be attached. When the seedlings are well established, the pots are sealed. This is done by first making a paper pattern and determining just where the hole to receive the stem is to be

bored in the cork. The cork is partly cut and then broken in halves and fitted about the stem. A little modeling clay may also be placed about the stem. This affords a waterproof seal and the plants may now be placed in groups in the several habitats. It is best to place the containers in the ground nearly level with the surface of the soil and if the weather is hot the metal tops should also be insulated with soil, dead leaves, or other materials. By reweighing at intervals of a few days, the relative transpiration in the several habitats may be determined. If the original leaf area and dry weight of a few of the seedlings in other containers are determined at the time the experiment is begun, growth at the end of the period may be measured in terms of leaf area and dry weight.

FIG. 177.—Sunflower phytometers used for measuring rate of transpiration, increase in dry weight, etc., in a field of sunflowers. All were seedlings when placed in the field; the two in the middle at the level of the surrounding plants, the two on the right below, and the two on the left above this level.

Table 6 gives the results obtained from 12 phytometers of green ash (*Fraxinus*) seedlings placed in a sumac thicket, in the adjoining prairie, and in the tension zone between the two. respectively, during a period of 8 days in midsummer.

Table 7 shows the average responses of sunflower phytometers in the same habitats during another period of 6-day's duration.

By the use of similar phytometers of bur oak and other tree seedlings, it was found that transpiration in an oak forest in Minnesota was less than half of that in a hazelnut thicket, and the water loss in the latter less than a third of that in the prairie.[574]

Since phytometers are often placed in habitats that make extreme demands upon the plants, it is best to use species that are as hardy and vigorous as possible. If the leaf area is to be measured, species with

simple, entire leaves or large leaflets are to be preferred. Sunflowers, beans, the smaller cereals, various tree seedlings, or similar native species have been found most satisfactory. Sometimes the plants are attacked and ruined by grasshoppers or June beetles or in other ways.

TABLE 6.—WATER LOSS FROM PHYTOMETERS OF TREE SEEDLINGS

Number of phytometer	Water loss, grams	Leaf area, square inches	Water loss, grams per square inch	Average loss, grams per square inch
Sumac thicket				
1	28.5	13.05	2.2	2.50
4	24.0	9.15	2.6	
7	10.5	4.85	2.2	
10	34.0	11.20	3.0	
Tension zone				
2	14.5	4.65	3.1	3.25
5	17.5	4.80	3.6	
8	22.5	7.60	3.0	
11	30.5	9.30	3.3	
Prairie				
3	37.5	6.40	5.8	5.72
6	45.5	6.65	6.8	
9	65.5	12.30	5.3	
12	62.0	12.35	5.0	

TABLE 7.—TRANSPIRATION AND GROWTH OF SUNFLOWERS IN THREE HABITATS

Responses	Sumac thicket	Tension zone	Prairie
Water loss, grams	133	611	802
Increase in leaf area, square inches	56	66	74
Increase in dry weight, grams	0.76	1.89	2.44

Sod-core Phytometers.—Water loss from various types of grassland has been measured by means of fitting metal cylinders, 1 square foot in cross-section and 3 feet long, tightly over undisturbed cores of sod and sealing the bottoms in place. The phytometers were then placed in holes just large enough to contain them, which were surrounded by undisturbed vegetation. The short-grass plains community lost water at an average rate of approximately 1 pound per square foot per day. In mixed prairie, where the vegetation is much more luxuriant, the loss was

1.3 pounds, and in true prairie, where conditions are much less xeric, about 0.85 pound per square foot.[570]

Free Phytometers.—Phytometers are not confined to plants sealed in containers, but may also consist of transplants or plants grown from seeds, etc. These are subject to the complete factor complex of the habitat and are thus unlike sealed phytometers where the factors of the soil are under control. Some degree of control may be secured, however, if desired, by watering, shading, thinning, etc. Planting in different situations to determine the comparative behavior of seedlings has been

FIG. 178.—Bundles of barley from representative square meters from field plots. All are from the same lot of seed planted at the same time in fertile soil: left, in eastern Colorado; center, north central Kansas; and right, eastern Nebraska.

practiced chiefly by foresters. Douglas fir in Arizona, for example, succeeds better under a cover of aspen than in the open, probably because of decreased transpiration, as indicated by the fact that evaporation was 50 to 90 per cent less.[382] The difficulty of establishment of prairie species in the short-grass plains and forest trees in prairie has been fully demonstrated by seedling phytometers.[98] In these studies, transplant phytometers consisting of large blocks of sod were also widely employed. The behavior of upland species in swamps or bogs and species of wet soil in well-drained areas can best be studied by means of reciprocal transplants. The responses of plants to different degrees of alkali or to acid soils may be similarly determined. In some cases (community phytometers), square meters of soil to a depth of 8 inches have been moved from

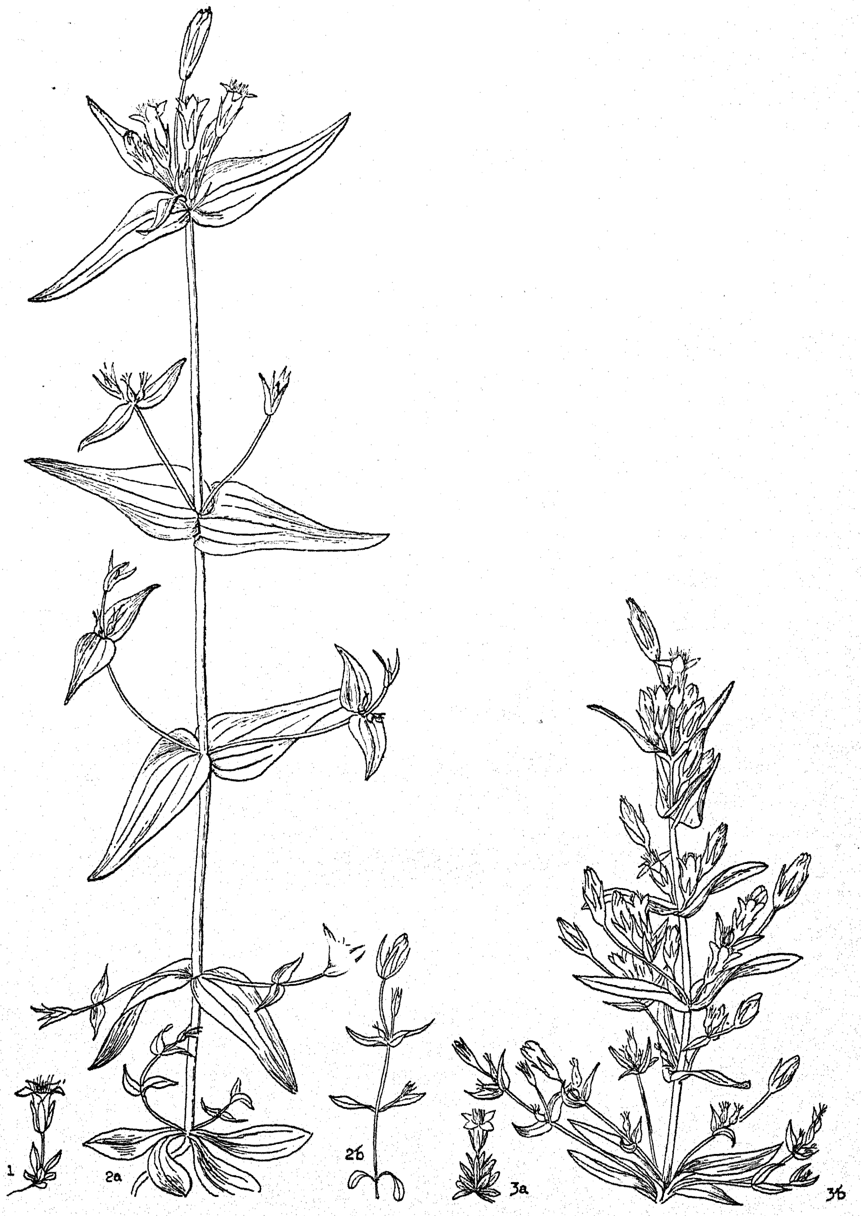

FIG. 179.—Adaptation forms of the rose gentian (*Gentiana amarella*). (1) alpine dwarf; (2*a*) normal shade; (2*b*) dry shade; (3*a*) drouth; (3*b*) normal sun.

one habitat into another and the effects upon the vegetation studied. In such cases, the control community, after being excavated, is again planted in its own habitat.[98]

Phytometers have been extensively used in measuring climatic conditions[317,345,434] (Fig. 178). The clipped quadrat is a type of phytometer, and the phytometer method is being employed in all experiments where plant production is used as a measure of environment.[563] Extensive studies of the adaptations shown by alpine plants when transplanted at lower elevations and lowland plants in various mountain habitats are throwing much light upon the whole problem of the origin and differentiation of species.[39,96] (Fig. 179).

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CHAPTER XV

ADAPTATION TO WATER

In nature, there are many types of habitats as regards water content. But no plants can ecize in both very wet and extremely dry situations. Each species flourishes only in those habitats where it finds a suitable water relation.

Types Produced by Adaptation to Water.—In the course of evolution, many species have become adapted in both structural and physiological features to habitats with an excessive water supply. Plants that live wholly or partly submerged in water or in very wet places are known as *hydrophytes* (Gr. *hudor*, water; *phyton*, plant). Plants of ponds, streams, and other bodies of water both fresh and salt, as well as those of swamps and wet meadows, belong to this group.

By far the greatest number of plants live in an environment that is characterized by a medium water supply, such as is found in the important agricultural districts of the temperate zone as well as in moderate altitudes in parts of the tropics. The plants of forests, meadows, and prairies usually belong to this group. Plants of habitats that usually show neither an excess nor a deficiency of water are known as *mesophytes* (Gr. *mesos*, middle; *phyton*, plant). In general, definite structures for increasing water supply or decreasing water loss are either slightly developed or completely absent.

Plants that grow habitually where the evaporation stress is high and the water supply low show characteristic adaptations to a decrease in water content. They are termed *xerophytes* (Gr. *xeros*, dry; *phyton*, plant). Plants of deserts, alpine peaks, sandhills, plains, table-lands, and high prairies usually belong to this group. As among hydrophytes, plants of this group include species from many families entirely unrelated phylogenetically, although some, as a result of the impress of the environment, have come to resemble each other more or less closely in vegetative characters, such as various cacti in arid portions of America and certain spurges in African deserts.[370] Likewise, the vegetation of the Arctic region resembles that of the Antarctic in its general physiognomy, although the two areas have practically no species in common.

Hydrophytes, xerophytes, and mesophytes are readily distinguishable as groups, since each has a more or less definite habitat and characteristic appearance. Between hydrophytes and mesophytes on the one hand, and extreme xerophytes and mesophytes on the other, there are found

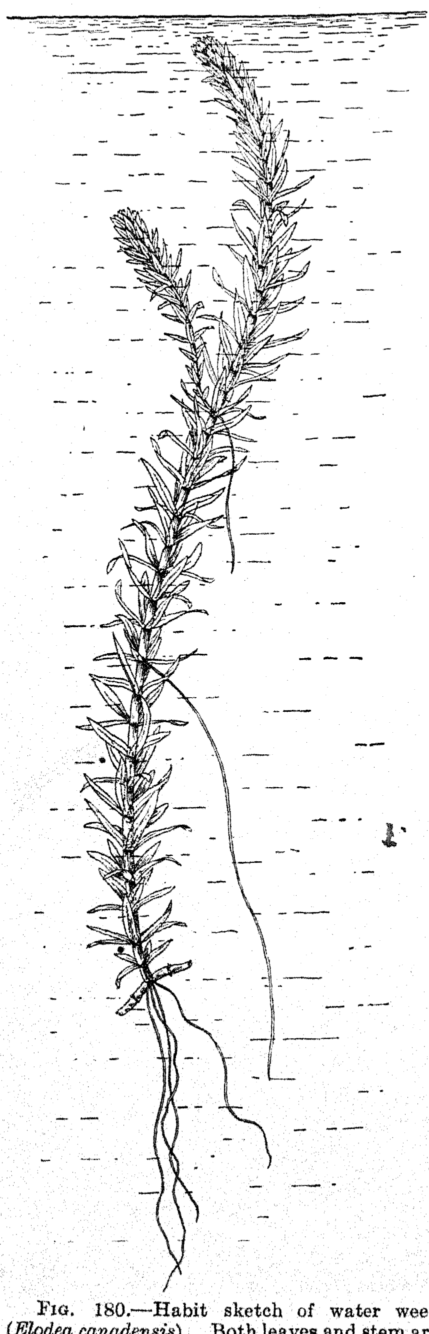

FIG. 180.—Habit sketch of water weed (*Elodea canadensis*). Both leaves and stem are green and the roots also contain chlorophyll if they receive sufficient light.

all gradations of form and all degrees of structural adaptations due to intermediate or partial habitats. Partly on account of the influence of humidity and partly because many habitats pass very gradually into each other, it is impossible to establish an absolute correspondence between each group and the water content.

HYDROPHYTES

Typical hydrophytes grow in water, in soil covered by water, or in soil that is usually saturated. With respect to their relation to water and air, they may be arranged into three fairly natural groups, *viz.* submerged, floating, and amphibious plants. Since the aquatic environment everywhere shows great uniformity, hydrophytes, and particularly the submerged and floating forms, show fewer adaptations than plants living under the more variable habitat characteristic of xerophytes. The structural adaptations are chiefly in response to excessive water content, which, of course, implies a decreased oxygen supply.[164] They consist of a decrease of tissues protecting from water loss and mechanical injury, a decrease in supporting and conducting tissues, and a marked increase in aeration of the tissues with a corresponding decrease in palisade (Figs. 180 and 181).

Submerged Plants.—Plants growing entirely submerged show

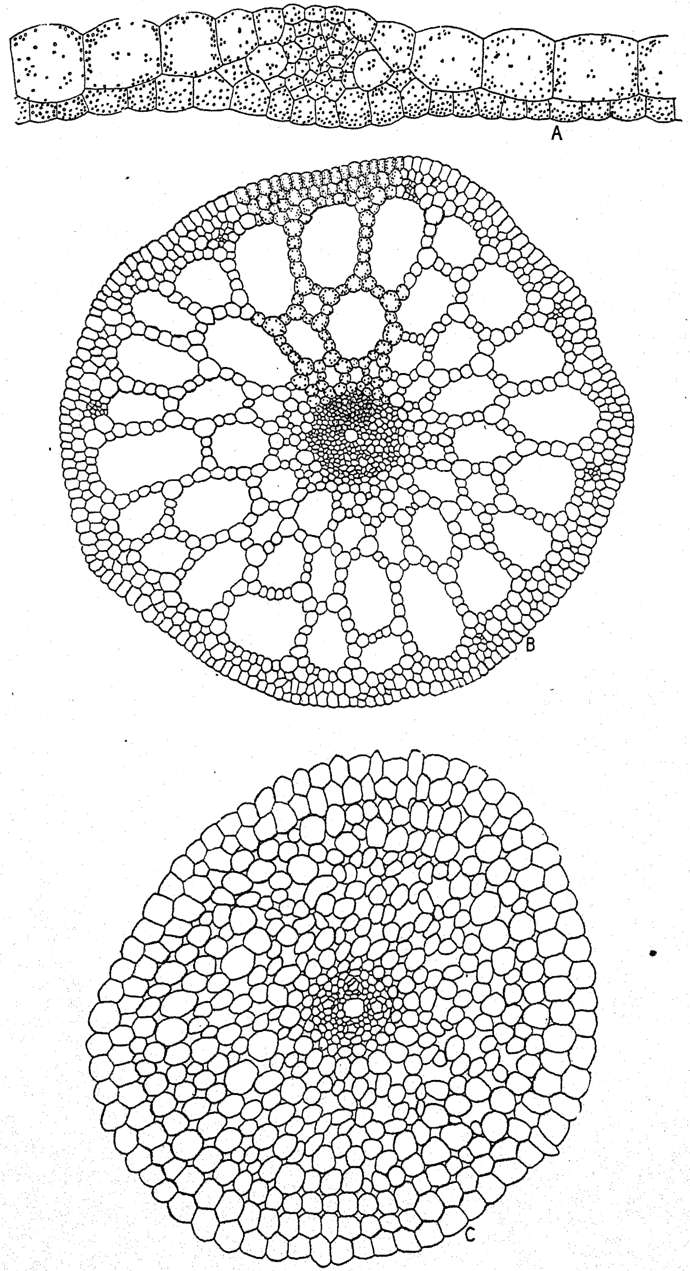

FIG. 181.—Detail of Elodea. *A*, cross-section of a leaf showing the much reduced fibrovascular bundle. *B*, cross-section of stem. Note the chloroplasts in the epidermis and the abundance of aerenchyma throughout the relatively large cortex. The stele consists entirely of thin-walled cells which are not differentiated into xylem and phloem. An intercellular passage occupies the center of the stele. *C*, a cross-section of the root

the greatest variations from the usual form and structure typical of mesophytes.

Ecological Anatomy of Submerged Plants.—A thorough understanding of the profound changes brought about by the water environment can be had only by a study of representative specimens.

Stems

Cut transverse sections of the stem of a submerged species of pondweed (*Potamogeton*) or other submerged hydrophyte and compare it with a typical mesophyte, such as a sunflower, in the following respects:

Epidermis.—Is there any cuticle or are all parts readily permeable to water? Compare the rapidity of wilting in portions of stems of the two plants when exposed for a time to the air. Do the epidermal cells contain chloroplasts?

Cortex.—Explain the relative proportion of the stem occupied by cortex and stele in the two species upon an environmental basis. Compare, also, the relative amounts of intercellular space and depth to which chlorophyll extends. Is there any collenchyma in the submerged plant? Stain with iodine and note where starch is most abundant and give reasons for this.

Central Cylinder.—Are there any fibrovascular bundles or any tracheary or fibrous tissue? The air space in the center of the stem marks the normal position of the xylem (Fig. 181). Explain these modifications on an environmental basis. Make a drawing about 4 inches long of one-fourth of the cross-section, showing all its parts. Examine sections of the stems of the hornwort (*Ceratophyllum*) or of *Najas*, *Zannichellia*, etc.

The structure of the stem of water milfoil (*Myriophyllum*) a part of which grows in the air above water, should also be examined and compared with the preceding plants in regard to each of the preceding characters. The relatively undifferentiated vascular strand should be noted.

Leaves

Examine and compare the leaves of *Potamogeton* in detail with those of a mesophyte in regard to epidermal characters, vascular bundles, and mesophyll. Draw a cross-section, filling in the chloroplasts. Also, cut sections of the leaves of any of the other submerged species. How do these compare with leaves of mesophytes?

Roots

Examine the roots of *Potamogeton*, or other submerged species which possess them, and compare them in regard to size, branching, root hairs, and internal structure with those of typical mesophytes. Compare those growing in water with those growing in soil.

The roots, stems, and leaves of higher plants of this ecological group are greatly modified. The epidermis of all of these organs is non-cuticularized and is thus able to absorb gases and nutrients directly from the water. The roots are greatly reduced in size, poorly or not at all branched, and destitute of root hairs except where they grow in the mud. In some species (*e.g.* *Ceratophyllum*), they have entirely disappeared. The older portions do not become impermeable with age, *i.e.* suberized or cutinized, as in land forms, but absorb throughout their entire life. Even in wholly submerged plants that are rooted, at least part of the

water and nutrient materials are often obtained from the soil. Plants growing in the same body of water make a better development when rooted in a rich, humus-filled soil than where they grow in sand.[536] Experiments have shown that many species can not secure enough of certain nutrients to make the usual vigorous and continued growth unless they are rooted in the substratum.[60,396]

The greater density of the water as compared with air renders support less necessary, and the stems are usually long and slender with a poorly developed vascular region. The mechanical need for developing the vascular bundles near the periphery of the stem, as in mesophytes, so as to secure maximum rigidity, no longer exists. Consequently, the cortex occupies a much larger area in proportion to stele, an arrangement that greatly increases its photosynthetic activity. In many species such as *Elodea*, *Zannichellia*, and *Najas*, the fused xylem strands are reduced to a central intercellular passage which is surrounded by phloem.[207]

The leaves are greatly reduced in size and thickness.[117] Although water is much richer in carbon dioxide than is the air, diffusion is relatively slow. The absorbing surface is consequently greatly increased and the tissues brought into close contact with the source of supply by finely dissected or thin, linear, or ribbon-like leaves, often only two or three cells thick.[62] This adaptation may have resulted, in part, also, from mechanical stress due to moving water. Although sclerenchyma strands occasionally occur, especially along the margins of the leaves where they give tensile strength, the general absence of supporting tissue is shown by the collapse of the plant when it is removed from the water. The thin leaves present an increased surface in proportion to tissue involved, for the reception of the diffuse light. The plastids are usually large and motile. Stomata are absent, except where vestigial, and these are functionless.

The chlorenchyma of both leaves and stems is of the shade or sponge type. In the few cases where both palisade and sponge are present, they are, doubtless, relics of a former structure. The epidermal layers, unlike those of land plants, are best supplied with carbon dioxide and frequently contain the chloroplasts most abundantly. Air chambers and passages filled with gas are common in all the vegetative organs, *i.e.* aerenchyma tissue is abundant.[208] They consist of regular spaces extending through the leaf and often for long distances through the stem. These spaces are usually separated by partitions of chlorophyll-bearing tissue only one or two cells in thickness. The air spaces not only afford buoyancy but also retain some of the oxygen resulting from photosynthesis to be used in respiration. Likewise, a part of the carbon dioxide that accumulates in these reservoirs at night may be used when the plant is illuminated.

Vegetative reproduction is highly developed and flowers and seeds are less abundant than in most habitats, a response found in most types of aquatic plants. *Elodea*, for example, reproduces rapidly by fragmentation; *Eichhornia* by runners; and duckweeds (*Lemna*, *Spirodela*, etc.) form new thalli so rapidly that under favorable conditions for growth they may soon cover the surface of a pond (Fig. 182). When sexual reproduction in submerged plants does occur, the flowers are usually fertilized at or above the surface of the water.[595]

These changes in plant structure have come about by change to an aquatic environment, as is shown by the fact that when mesophytes are grown under very moist conditions there is a pronounced increase in

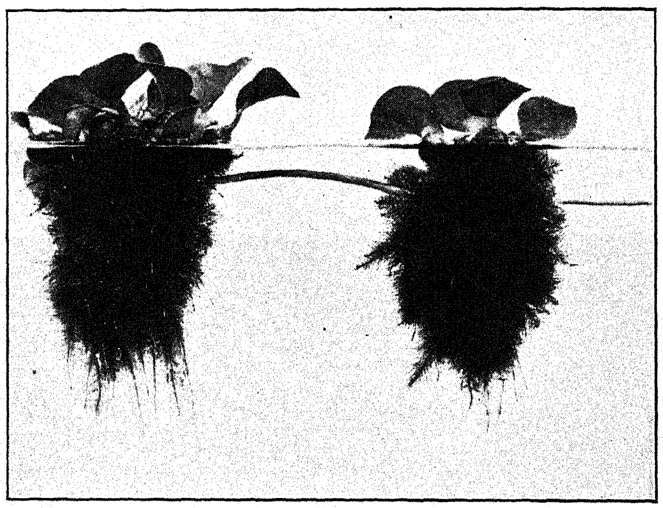

FIG. 182.—Water hyacinth (*Eichhornia*) propagating by runners. The bladder-like floats are the enlarged air-filled petioles.

intercellular space. If the stems are submerged, they often develop large air cavities by the breaking down and separation of certain groups of cells in the cortex. Very plastic plants like water smartweed (*Polygonum amphibium*) when grown in dry soil have rough, hairy stems and leaves, but when developed in water these are quite smooth throughout.

Floating Plants.—Plants of this group have undergone striking modifications in form and structure; even the aerial parts show their close association with the water habitat.

Ecological Anatomy of Floating Plants.—Examine various free-floating forms such as duckweeds (*Lemna*, *Spirodela*, or *Wolffia*), water hyacinth (*Eichhornia*), and water fern (*Salvinia*). Why do they not become wetted when plunged under water? Note the method of vegetative propagation in the duckweeds where each thallus or frond represents an individual plant. How does *Eichhornia* propagate vegetatively? Cut

sections of the thallus of a duckweed, the swollen petioles, and leaves and stems of water hyacinth and explain why each kind of plant floats. In cold water in late autumn duckweeds form winter buds which have more compact tissues than the thalli produced earlier in the season. Being heavier than water they sink to the bottom of the pond where they remain alive until spring, while those that remain afloat freeze.

Examine the roots with regard to branching habit, root hairs, and the conspicuous root pockets that fit over the ends of the roots. Are these of any advantage to the plant?

Examine the floating leaves of various species of water lilies (*Nymphæa*, *Castalia*), lotus (*Nuphar*), or water shield (*Brasenia*). Examine and draw cross-sections of the leaves showing the stomata, air spaces (ærenchyma), and sclereids. Of what are sclereids composed and what is their function? Why is it essential that the leaves of floating plants be not easily wetted? How is this protection accomplished in the water lily? Does the petiole give the leaf mechanical support? The stems consist usually of thickened rhizomes rooted in the mud. Would you expect the petiole to have some vascular elements for the conduction of water, nutrients, and food? Examine sections under the microscope.

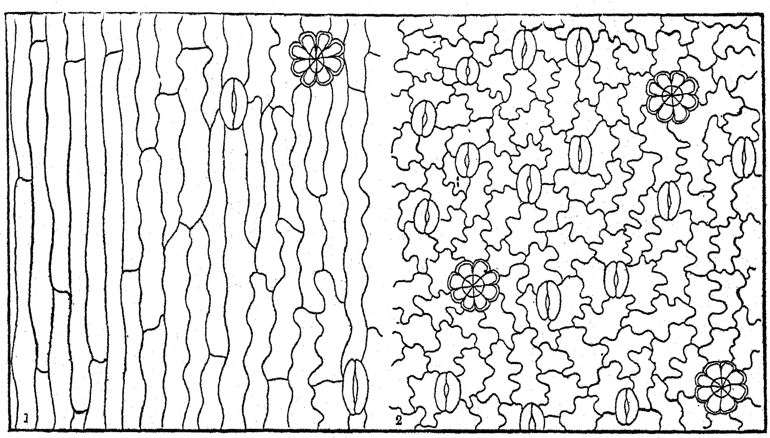

FIG. 183.—Upper epidermis of (1) a submerged leaf and (2) of an aerial leaf of northern water starwort (*Callitriche bifida*), showing the decrease in the number of stomata.

Many species of this group are free-floating forms, others are rooted in the mud and only the leaves and flowers float on the surface of the water. In the *Lemnaceæ*, where the leaf and stem are represented by a tiny thallus, the roots are in the process of disappearing. *Spirodela* has several, *Lemna* but one, and *Wolffia* none. Such typical water roots are hairless. In addition to having the characters described for those of attached, submerged plants, they possess root pockets. The function of these enlarged rootcap-like structures is not so apparent as is the rootcap of terrestrial plants.

Most attached species (water lilies, pondweeds, etc.) develop long, horizontal stems, rootstocks, or tubers. By means of these, they migrate rapidly through the water or mud and, as a consequence, the

plants usually form conspicuous communities. The root systems are poorly developed, probably as a result of an excess of water and the reciprocal diminution of air. The petioles are much elongated. The aerating system is greatly emphasized, and supportive tissues, such as fibrovascular bundles, are reduced. The leaves that have developed under water are like those of submerged plants, but in both form and structure of the upper portion, floating leaves are essentially similar to those of amphibious plants. They are usually coated with wax which prevents the wetting of the upper surface and the clogging of the stomata by water. Stomata are found only on the upper surface, with the exception of a few cases where they persist with loss of function upon the lower side (Fig. 183). The palisade tissue of the leaf is often well developed, but is usually exceeded by that of the sponge tissue which is filled with large air chambers (Fig. 184).

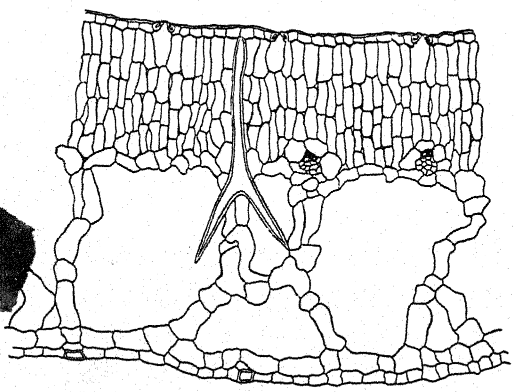

FIG. 184.—Cross-section of the leaf of a water lily (*Nymphaea advena*). Note the stomata in the upper epidermis and the slime glands in the lower one, also the large Y-shaped, thick-walled sclereid which probably furnishes mechanical support. Photosynthetic activity is confined to the upper half of the leaf, the large, air-filled lacunæ in the lower p[illegible]ng buoyancy.

Amphibious or Emersed Plants.—Plants of this group are adapted to live partly in water and partly in air. The two partial habitats are very different and usually the response of the plant is marked.

Ecological Anatomy of Amphibious or Emersed Plants.—The cattail (*Typha latifolia*) is a good representative of this group (Figs. 185 and 186). Cut sections of the thick rhizome and examine for relative proportion occupied by cortex and stele. In the cortex, note the thickened endodermis, columns of bast fibers, and occasional bundles, together with the well-developed aerenchyma, and hypodermis of thin-walled parenchyma.

Examine cross-sections of roots. What effect has decreased water content and increased aeration upon root branching and root-hair development (p. 231)?

Examine sections of freshly cut leaves and, later, prepared slides of the same. Make out clearly, by cutting the leaves lengthwise, the nature and position of the

I-beams and diaphragms separating the large air spaces. To what portion of the leaf is photosynthetic activity confined? Examine the structure of one of the I-beams in detail.

Draw an aerial and a submerged leaf of some heterophyllous species such as yellow water crowfoot (*Ranunculus delphinifolius*), mermaid weed (*Proserpinaca palustris*), water cress (*Roripa americana*), etc. Examine the changes in size and structure of aerial and submerged leaves of species of water starwort (*Callitriche*) or mare's-tail (*Hippuris*).

Most species of amphibious plants have extensive underground or creeping stems which are rooted in the mud and spread rapidly. Thus, while the roots and portions of the stem as well as frequently part of the leaves are under water, at least a portion and often most of the shoot is aerial. Plants of tidewater marshes and other places subject to periodic inundations belong to this group. In addition to numerous vascular plants, many algæ are also included here. In fact, some of the latter can not live if they are constantly under water.

The vascular species of this group are closely related to mesophytes and are the least specialized of water plants. Owing to their frequent occurrence at the water's edge, many amphibious plants have a wide range of adjustment and may grow for a time as mesophytes or partially submerged.

The roots exhibit the usual characters of plants growing in water-logged soil. Their extent, degree of branching, and root-hair development vary directly in proportion to decrease in water content and increase in aeration (Fig. 126). Owing to variation in the water content of marsh habitats, the rhizome structure may show both hydric and xeric adaptations. In *Typha*, for example, the prominence of mechanical and conductive tissue indicates mesophytic tendencies; the abundance of storage parenchyma and aerenchyma, hydrophytic ones.[229,597] The thickened endodermal layer affords a means of protection against water loss during drought. Since both mechanical and conductive tissues are well developed, the plants are able to grow erect without being supported by the water. Perhaps the most distinctive feature of the stems of amphibious plants is the large internal air chambers crossed by frequent diaphragms that are pervious to air.[502] These are important in affording aeration to the submerged parts, as may be shown by an experiment in which all of the rootstocks are cut at the water's edge and the aerial shoots below the water level. In most cases, the plants will not recover. Submerged portions of seed-bearing hydrophytes are often covered with slime which harbors communities of bacteria, etc.

The leaves of amphibious plants show the greatest variation in both form and structure when the plant is subjected alternately to the air and water environment. The lower leaves of some species are covered, either normally or by a rise in water level. When they develop under

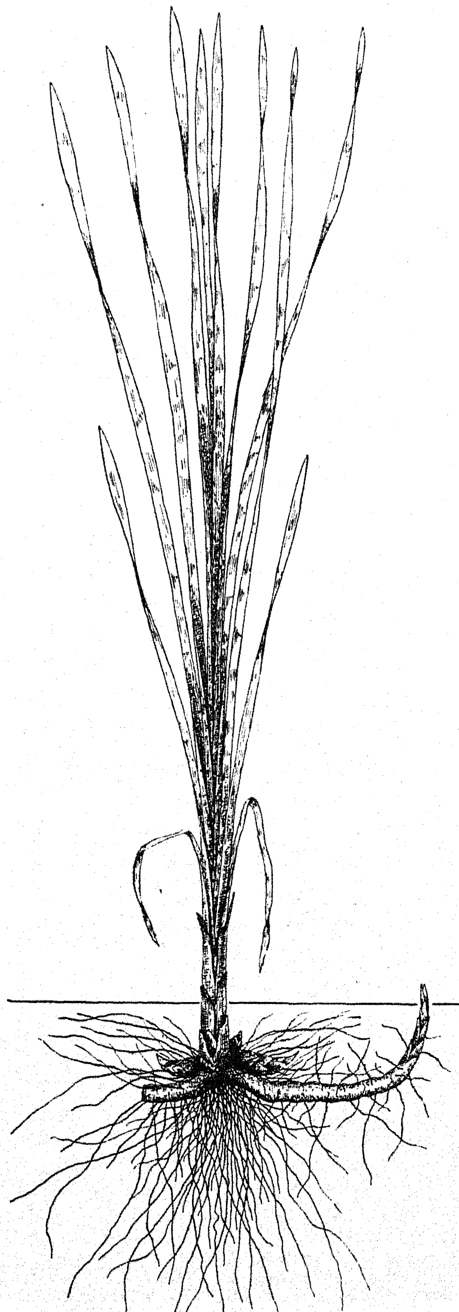

FIG. 185.—Habit sketch of cattail (*Typha latifolia*).

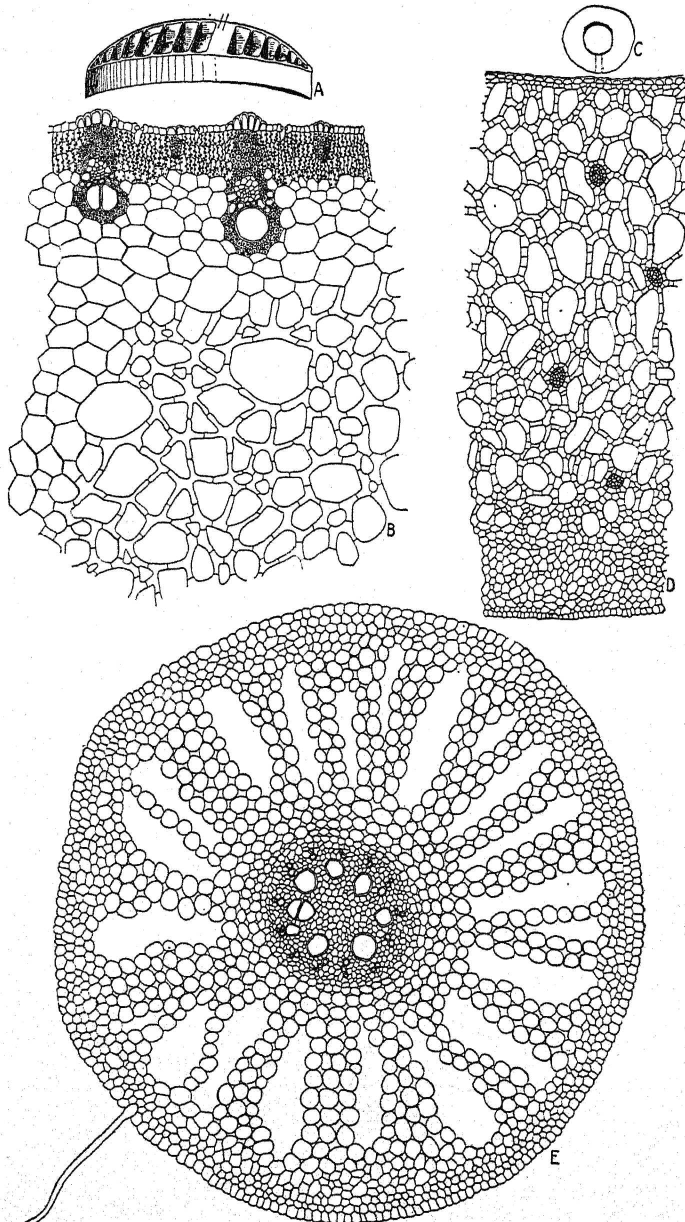

FIG. 186.—Detail of structure of *Typha latifolia.* *A*, section of leaf showing I-beams, air chambers, and diaphragms. The parallel lines indicate the position of the portion greatly enlarged in *B*. *C*, outline of a cross-section of a rhizome showing relative proportion of cortex and stele and the part shown in detail in *D*. *D*, the epidermis, consisting of a single layer of cells; endodermis consisting of many small cells; aerenchyma and columns of bast fibers; and thick-walled endodermis. *E*, cross-section of a root showing abundance of aerenchyma.

water, they take the form and structure of submerged leaves. The aerial leaves are usually large and entire, showing a marked tendency to increase the exposed surface (Fig. 187). This is clearly shown by experiments with *Ranunculus sceleratus* grown under varying conditions of water content. Floating leaves and those of plants grown in saturated soil are larger than those on plants grown in drier soils, but they change little or not at all in thickness. The lake cress (*Radicula aquatica*), water crowfoot (*Ranunculus aquatilis*), and mermaid weed (*Proserpinaca palustris*) are representative. Changes in size and structure without dissection of the leaves are shown in some species of pondweed (*Potamogeton*), water starwort (*Callitriche autumnalis*), and others. Many species are less plastic.

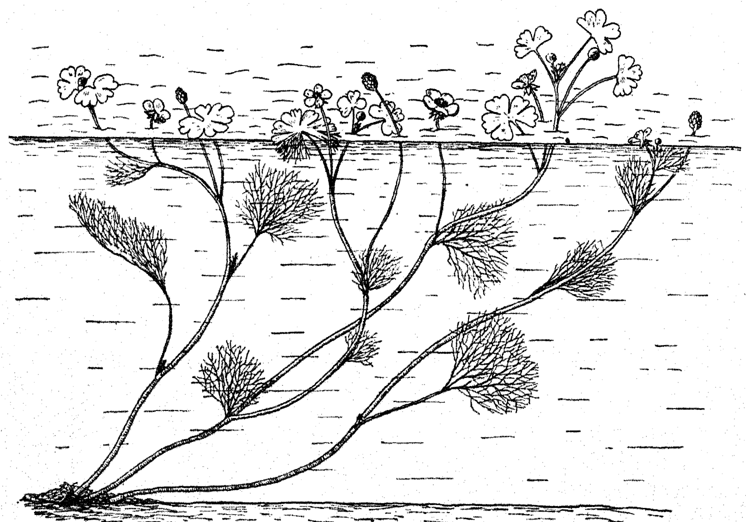

FIG. 187.—Habit sketch of a water crowfoot (*Ranuculus aquatilis*).

The change in the form and structure of the submerged leaf seems clearly related to the absorption of carbon dioxide from the water, there being no danger of drying. As soon as the leaves begin to develop above the water surface, they meet the danger of desiccation by the production of a cuticle and the necessary accompanying stomata. In a plant such as *Ranunculus aquatilis*, these changes may be brought about at will by growing portions of the plant in air or in water. Where stomata are present, they have only slightly cutinized walls and in most hydrophytes are almost always open, many species such as *Typha* and *Scirpus validus* having lost the power to close them even in extreme wilting.[320] Compared with mesophytes, the cuticle is usually thin and destitute of hairs.

The stomata are numerous and usually more abundant on the upper than on the lower surface. The palisade tissue is represented by one or

more well developed rows, but this portion of the leaf is regularly thinner than the sponge parenchyma. The sponge tissue contains large air spaces or numerous large air chambers, usually provided with thin plates or diaphragms of cells. The palisade is reduced as the air spaces and sponge tissue increase. Hence, the chloroplasts are exposed more completely to the sunlight, and water loss is augmented. The fibrovascular system is more efficient than in other types of hydrophytes.

An explanation has recently been proposed which satisfactorily accounts for the origin of a cuticle in land plants and in parts of hydrophytes exposed to the air. It also reveals why a cuticle is absent in absorbing roots and in all submerged parts of hydrophytes. Meristematic tissues always contain fatty substances, such as fatty acids, fats, and lipins, which migrate to the plasmatic interfaces during the processes of vacuolation and differentiation. Subsequently, they migrate into and along the walls separating the protoplasts until they reach the surface of the root or shoot. Sodium, potassium, and magnesium soaps of fatty acids move quite readily along cellulose walls saturated with water, but calcium soaps are immobile. Many of these fatty substances contain unsaturated fatty acids which are liable to undergo rapid change in the presence of oxygen, oxidizing and condensing into varnish-like substances insoluble in water. Thus, the cutin of the cuticle is formed. Cutin is merely a name for an aggregate of substances varying in specific composition but having the same general characters, most important of which is their low permeability to water. In submerged plants the fatty substances pass on into the surrounding water (unless it is predominately calcareous, when insoluble calcium soaps may accumulate) and are never oxidized, that is, ordinarily no cuticle is formed. The absence of a cuticle on absorbing water roots or soil roots is similarly explained. Conversely, where large intercellular spaces occur, as in hydrophytes or in the cortex of the roots of many plants, the endodermis may be quite waterproofed, except for passage cells, by oxidized fatty acids forming cutin or suberin.[305]

MESOPHYTES

Mesophytes grow in habitats that are neither extremely dry nor wet. The oxygen supply about the roots is moderate, the solutes are neither extremely dilute nor too concentrated. Because of variation in light, however, mesophytes are differentiated into sun and shade forms. A mesophyte possesses a form or structure that is more or less characteristic by reason of the absence of distinct modifications. Notwithstanding its apparent lack of a distinctive impress, a mesophyte is as much a product of its habitat as the well-marked hydrophyte or xerophyte.[343]

Mesophytes stand midway between hydrophytes and xerophytes. For this reason, they pass, on the one hand, into dry land plants and, on

the other, into amphibious plants. Various xerophytes and hydrophytes have, moreover, often found themselves in conditions that changed them into mesophytes. Many of them have, in consequence, retained characters of leaf, stem, or root that are to be regarded as ancestral rather than as the result of adaptation to the present habitat.

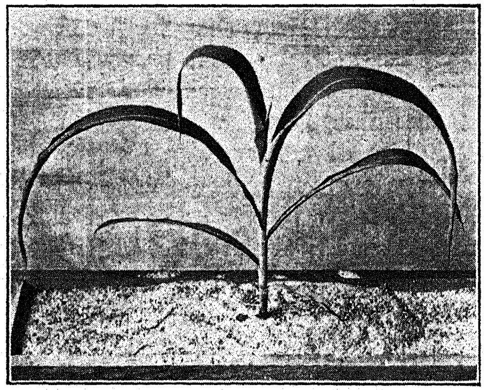

FIG. 188.—A corn plant (*Zea mays indentata*) with leaves rolling as a result of drought.

The roots of mesophytes, such as common field and garden crops, plants of meadows, and species of deciduous and moist evergreen forests, are usually extensive and much branched. Root length, except perhaps in the case of trees, usually equals or exceeds the height of tops, and the volume ramified by roots likewise usually equals and often greatly exceeds that occupied by the aboveground parts. Root hairs

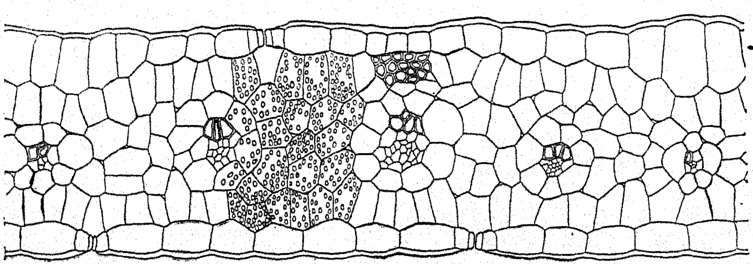

FIG. 189.—Cross-section of a leaf of corn showing two groups of the enlarged bulliform (bubble-like) cells in the upper epidermis. These constitute the rolling device. Upon loss of turgidity in these cells the leaf rolls inward.

are nearly always abundant. Conditions for humus accumulations are favorable, bacteria and fungi are plentiful and often intimately associated with the roots in nodules or as mycorrhiza.

The foliage of mesophytes shows a maximum development. The leaves are large and of moderate thickness (Figs. 188 and 189). Due to the thin, transparent epidermis, which is moderately cutinized, and an

abundant development of chlorophyll, they are of a deep-green color. This is quite in contrast to many xeric species. The stomata are abundant and, except in trees, usually distributed on both surfaces (Fig. 190). They are relatively uniform in structure, and the guard cells show a maximum capacity for movement. The rate of water loss is usually intermediate between that of hydric and xeric species, at least when this is measured under similar environmental conditions[54,375] (Fig. 191).

To Determine the Relative Rate of Water Loss of Hydrophytes, Mesophytes, and Xerophytes.—Select three plants of each of two representative species of the preceding groups and grow them in metal containers with provision for

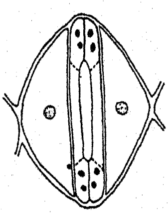

FIG. 190.

FIG. 191.

FIG. 190.—Surface view of an open stoma of corn showing guard cells with chloroplasts and the subsidiary cells with prominent nuclei. The ends of the guard cells are thin-walled and enlarged but the central parts next the aperture are thick-walled and rigid. When the bulbous ends of the guard cells become turgid and distended they press against each other thus forcing the rigid centers to separate and the stoma to open.

FIG. 191.—A group of hydrophytes, mesophytes, and xerophytes sealed in containers for measurement of transpiration losses. Three types of seals are shown. Under mesic conditions water losses per unit area were in the following sequence: cattails (greatest), beans, sunflowers, mullein, pine, and cactus.

aeration. *Typha, Eleocharis,* or *Scirpus* are easily grown from rhizomes. Beans, sunflower, or geranium may be used as representative mesophytes, and mullein, cactus, or pine are easily transplanted xerophytes. The plants should be transplanted into the containers (except those grown from seed) at least 6 weeks before determining transpiration, to insure that they are well rooted. The xerophytes thrive best in soil that is not too moist. After appropriate watering, seal each container with cork, modeling clay, or by means of a double layer of oilcloth, with the slits from the central opening for the stem extending in opposite directions, covering a mulch of dry sand. Weigh each to the nearest gram, and place the lot together under mesic conditions for 1 week. Watering, if necessary, should be done from a graduate and the amount of water used

recorded. At the end of the period, after the second weighing, make leaf prints and determine the transpiring surface, preferably by means of a planimeter. The surface of the stems of the leafless species and the pine needles should also be determined. Finally, arrange the species according to the rate of water loss in grams per square decimeter.

XEROPHYTES

It has been shown how the functional responses of plants to an excess of water produce modifications in form or in structure or in both. That this modification may take place in root, stem, or leaf or in all of these organs has also been observed.[149] In xerophytes, which show response to a decreased water content and humidity, modification is greatest in the leaf. This is the organ of greatest activity and of greatest exposure to the drying power of the air. The factors of xeric habitats operate upon the stem somewhat in proportion to the degree that it carries on the functions of a leaf. The root is probably changed least, owing to the more uniform conditions of the soil environment as well as to its fewer activities. Just as roots frequently fail to develop when stem and leaves do their own absorbing, so, also, when the water supply is reduced to a minimum, leaves may be lost (Fig. 192). Xerophytes are much greater in number of species and more diversified in form, structure, and physiological adaptations than are hydrophytes.

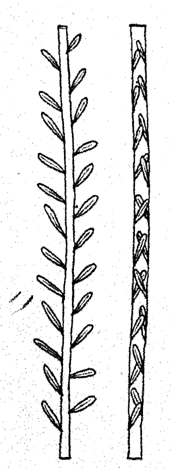

FIG. 192.—Portion of a compound leaf of the horse bean (*Parkinsonia aculeata*), showing the reduced leaflets which may fold against the broad, green, wing-margined petiole (natural size).

Types of Xeric Environments.—Xerophytes are the characteristic plants of deserts, but they are by no means confined to them. They may occur in any habitat in which low water content is accompanied by atmospheric conditions which promote rapid water loss. Structural and physiological modifications common to xerophytes have been evolved under many different degrees and kinds of xeric environments. In fact, several types of deserts are readily distinguishable. First are those with very low rainfall and a hot, dry, windy climate such as is characteristic of the thorn-scrub deserts of the southwest. In contrast is the less xeric *Artemisia-Atriplex* type of the West and Northwest. More extreme than either, and almost if not quite excluding all types of plant growth, are the alkali deserts in which aridity is supplemented by a soil with such an excess of salts that absorption from it is extremely difficult or impossible.

Similarly, halophytes growing in moist climates and frequently in water have elaborate xeric structures to reduce water loss. The high osmotic concentration of the soil solution makes absorption difficult. Unlike the physically dry soils where water is actually deficient, such

habitats are said to be physiologically dry. They are characteristic of salt marshes and tidal flats and occur inland about salt lakes, salt springs, etc.[42]

In Arctic and alpine regions, although water may be abundant, the soil temperature is so low that absorption is difficult. The characteristic plants of temperate and subarctic zones, such as gymnosperms, show xeric adaptations to this type of physiological drought, and mesophytes occur in abundance only where they are protected by snow from excessive water loss during dormancy.

Other types of xeric habitats such as plains, table-lands, etc., are xeric because of low rainfall, often coupled with high run-off and great evaporation. Rock ledges and cliffs afford local xeric areas, even in

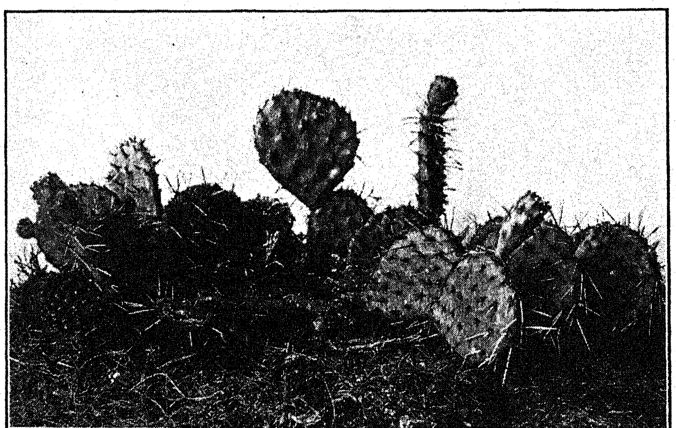

FIG. 193.—A drought-resisting plant. This cactus (*Opuntia camanchica*) has blossomed and the fruits, which appear as small branches, are ripening. The fleshy green stems in addition to storing water perform the work of leaves.

climates suited to mesophytes. Similarly, sandhills, dunes, sand-draws, etc., even along the Atlantic Coast, are, for a time at least, populated with plants of xeric habit. This is because of rapid percolation and shifting of the surface soil and, especially, the intense insolation at the soil surface.

Plants of xeric habitats have been classified as (1) drought escaping, (2) drought evading, (3) drought enduring, and (4) drought resisting.[276, 465] Annuals adapted to such a short growing season that they can complete their life cycle from germination to maturing seed during a brief period of water supply escape drought. The offspring is so well protected in the seed that it is immune from drought. Even the seeds of mesophytes show extremely xeric structures such as durable seed coats, compact tissues, and, when mature, very low water content. Although the development of certain structures varies with the habitat, such as lower permeability of seed coat of clover grown in dry climates, in general all

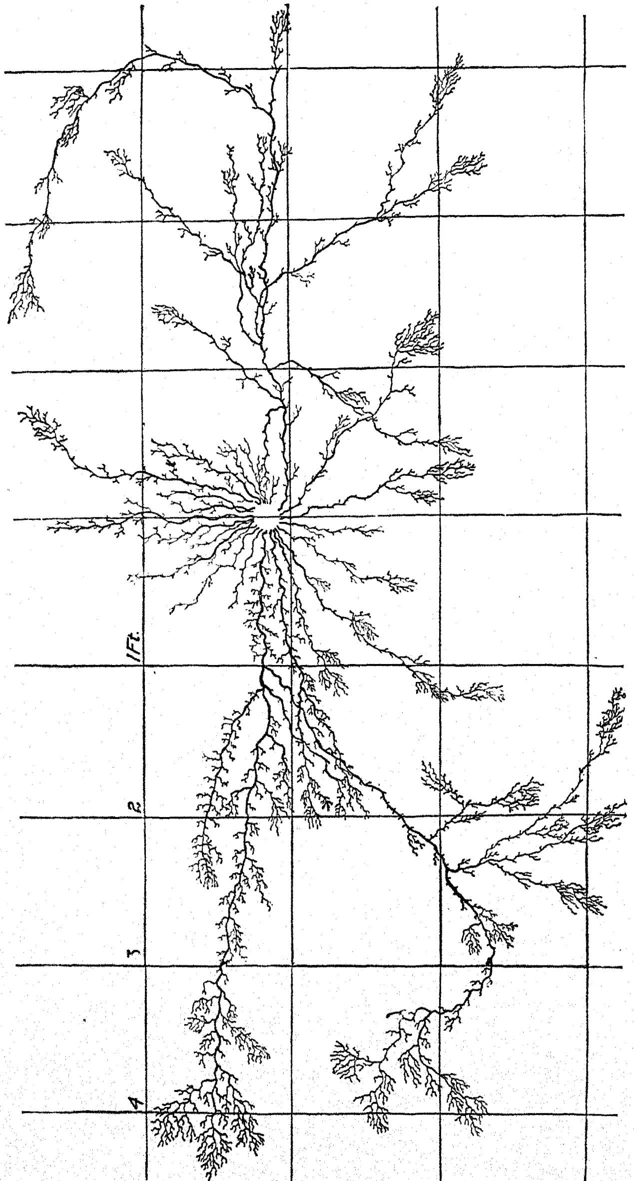

FIG. 194.—Top view of surface roots of cactus shown in Fig. 193. Scale in feet. Aside from three to five vertical roots which reach depths of 2 to 3 feet, the entire absorbing system occurs in the surface 1 to 4 inches of soil.

seeds are xeric. The second group of plants evade drought by conserving the scanty moisture supply as a result of small size, restricted growth, growing far apart, or low water requirement. Drought-enduring species, such as many desert shrubs, in addition to having most or all of the qualities of the preceding group, endure drought by passing into a condition of dormancy that is broken only upon the advent of a renewed moisture supply. The fourth group resists drought by accumulating a supply of water that is used when none can be secured from the soil. Here belong the cacti and other species with fleshy stems or leaves or roots. They are able to extend their root area even in dry soil and are thus better fitted to secure water when the soil is moistened[465] (Figs. 193 and 194).

Adaptations to a Decreased Water Supply.—A proper water supply is essential to the functioning of a plant. When this is greatly diminished, growth is retarded and the very existence of the plant threatened. The effect of a deficiency in the supply must be met by changes that decrease the demand arising from water loss or those that increase the supply by adding to the absorbing or storage capacity of the plant. These changes affect cell metabolism and result in modifying the form and size of various organs as well as their structure. Plants have become adapted to drier habitats both physiologically and structurally. In fact, there is increasing evidence that the products of the changed metabolism induced by drought directly account for certain structural changes.

Succulence.—This is one type of adaptation common to many species of desert and saline areas and is illustrated by cacti and the saltwort (*Salicornia*), respectively. The parenchymatous elements show an exaggerated development in relation to the more rigid tissues, these masses of thin-walled cells remaining distended and turgid. Succulence may originate as a direct result of aridity. The reduction of the water content of a cell below a certain point results in the conversion of polysaccharides, with a low imbibition capacity, into pentosans. The latter, especially when mixed with nitrogenous substances under the organization of the living plant, have a high hydration capacity, the action having the force of regulatory adjustment. Since the change is irreversible, the pentosans result in permanent succulence.[329,507] The presence of essential oils also reduces transpiration.

Thickened Walls.—Another form of xerophytism is expressed in thicker cell walls and protective coverings. These result from the accelerated conversion of the polysaccharides into their anhydrides or wall materials (celluloses, etc.). This metabolic change is also induced by a depleted or lessened water supply in the cells.[331] The result is that the plant structures take on the indurated qualities so characteristic of many desert species. Desiccation promotes the development of cork.[206,403] Even in mesophytes the advent of winter or extreme summer

drought usually results in the closure of the lenticels by the growth of a layer of cork. The thickness of bark varies with the habitat, usually being least in moist places and greatest in deserts, alpine regions, etc., where factors promoting desiccation are greatest. In plants of xeric habitats, the conducting tracts are also well developed. Not only are the vessels more numerous, larger, and longer, but also the walls are much thicker than in mesophytes. Lignification begins earlier and is pronounced, and the rings of growth, whether one or more a year, well developed. Bast fibers and sclerenchyma reach their highest development. Because of thicker epidermal coverings or deeper-seated chlorophyll, or because the chloroplasts are paler or fewer (as in cases of excess of salt), desert plants usually have a dull grayish color quite in contrast to the bright green of mesophytes and hydrophytes. This use, moreover, of carbohydrates in making wall materials, etc., is accompanied by a limited growth, particularly in stems and leaves where the effects of aridity are greatest. Hence, dwarfness is common among plants of xeric habitats. Frequently, it results in spinescence, which is also promoted by intense light and extreme desiccation.[601] The two types of transformation of carbohydrates, *viz.* the formation of increased cell-wall materials and hydrophilous colloids resulting in succulence, may take place in different parts of the same plant. In fact, wall materials are emphasized in the peripheral cells of cacti, for example, and pentosan and mucilage accumulation in the interior.

Osmotic Pressure.—An increase in osmotic pressure is another adaptation to drought. The concentration of the sap of a species is not constant. It may be influenced by any of the environmental conditions affecting transpiration, by the products of photosynthesis, or by the supply of available water. The sap density of any species usually shows variations corresponding to the degree of aridity of the habitat, the highest osmotic pressures, except in succulents, usually being found in more drought-resistant species. Among mesophytes, the osmotic pressure within the root hairs increases somewhat as the soil water becomes less and the solutes more concentrated. Likewise, the cell sap of the leaves, when the plants are grown in dry places, often shows an osmotic pressure greater by several atmospheres than that of similar plants in moist situations.[220,257]

Among xerophytes generally and especially woody species and plants of salty areas, high osmotic pressures usually prevail.[238] This is combined, in the plants of the latter group, with the ability to resist the toxic action of concentrated salts within the cell, which would undoubtedly be injurious to many other plants. Among evergreen trees and shrubs in Idaho, there has been found a gradual increase in the osmotic pressure of the leaves from midsummer until after the coldest weather of winter. Then the osmotic pressure again gradually fell to a minimum (Fig. 158). This is believed to be due to the cessation of growth during

midsummer, possibly as a result of drought, and the storage of the products of photosynthesis. With the oncoming of winter, the starches are gradually converted to sugars, oils, etc., the sugars causing the increase in the osmotic pressure.[174,351]

A correlation between plant succession and osmotic pressure has been shown in Utah, where one plant community gradually replaces another more tolerant to salt as the soil becomes less alkaline.[219] In the saline deserts about Great Salt Lake the succession in the sequence indicated in Table 8 is from the vegetation of the salt flats to sagebrush.[462] The osmotic pressure decreases gradually in each of the several stages from the initial one to the climax. The osmotic pressures are the averages for several woody species in each community, except the fleshy herbs in the salt flats. The table also shows the sequence of woody species with increased precipitation resulting from an increase in altitude.[292]

TABLE 8.—OSMOTIC PRESSURE IN PLANTS OF VARIOUS COMMUNITIES

Community	Osmotic pressure, atmospheres	Community	Osmotic pressure, atmospheres
Salt flats (*Salicornia, Allenrolfea*)	34.6	Piñon-juniper	21.4
Greasewood-shadscale (*Sarcobatus vermiculatus, Atriplex confertifolia*)	32.0	Oak brush:	
Shadscale (*Atriplex confertifolia*)	22.4	South slope	20.0
Sagebrush (*Artemisia tridentata*)	22.0	North slope	16.4
		Average	17.7
		Aspen-fir	15.0
		Spruce-fir:	
		South slope	15.0
		North slope	12.6
		Average	14.0

Other Changes.—In proportion to their tops, the roots of xerophytes are frequently greatly elongated, much branched, and densely clothed with root hairs. In a few cases, the latter extend to the root tips and possess thickened, lignified walls. The main roots of many species are much enlarged and serve as reservoirs for the accumulation of food and water.

In many species the leaves are greatly reduced or wanting, and in others the stem is so reduced that the leaves seem to spring directly from the top of the enlarged root. In such short-stemmed forms, the internodes are little or not at all developed and the rosette of leaves either lies flat on the soil surface or forms a hemispherical group of radiating and often more or less fleshy or bayonet-like leaves, as in certain species of *Agave* and *Yucca*.

Finally, many desert forms are of the annual-stemmed type. These herbaceous perennials develop rapidly during the short, moist or rainy season from rootstocks, tubers, bulbs, or corms that lie dormant during drought. They may expose foliage with mesic characteristics and flower and fruit abundantly, although many reveal characteristic xeric structures in both stems and leaves. Upon the advent of drought the entire top dies to the ground.

In addition to dwarfness of stem and leaf, compactness of tissues, heavy cuticularization and lignification, and an abundance of conductive and mechanical tissues, other changes in form and structure will be found as representative xerophytes are examined.

Adaptation of Leaves to a Small Water Supply.—Modifications in the form or size of leaves that reduce the amount of surface exposed to the air lessen transpiration. Changes of structure, on the other hand, are a means of bringing about the protection of epidermal cells and stomata as well as the internal tissues from the factors that promote transpiration. The stomata of xerophytes are generally in a state of partial closure. Water storage in specialized cells or tissues affords a reserve supply and is a means of tiding the plant over critical periods of drought. In a few extreme cases, the epidermis may be modified for absorbing water from the air.[210,591]

The modifications of leaves that serve to decrease water loss may be grouped under the following heads: (1) position of the leaf; (2) rolling or folding of the leaf; (3) reduction of leaf surface or loss of leaves; (4) changes of epidermal cells; (5) modifications of the stomata; and (6) changes in chlorenchyma. Naturally, some of these modifications are found in mesophytes, which frequently experience periods of drought. They occur regularly in xerophytes.

Decrease of Water Loss through Leaf Position.—Horizontal leaves receive much more radiant energy throughout the day than do vertical ones. Consequently, other things being equal, this horizontal position would result in the greatest water loss. Since the light is most intense when the sun is highest, it seems clear that those leaves would transpire least which make the smallest angle with the rays of the sun during the middle of the day. A leaf at right angles to the rays of the sun receives almost ten times as much light and heat upon the same surface as one placed at an angle of 10°. Reduction of water loss by means of the vertical or oblique position of the leaves is of frequent occurrence in the erect or hanging leaves of many tropical trees. A similar means is found in "compass plants," such as *Silphium laciniatum*, *Lactuca scariola*, etc., and in all species with more or less erect, hanging, or equitant leaves (*i.e.* overlapping as in the iris). Some species such as mullein (*Verbascum*) exhibit a leaf position varying from the horizontal to the vertical with increase in height from the soil and correspondingly increased

evaporation stress. The effect of leaf position on water loss, however, is just opposite in the sunflower and other heliotropic species, since the

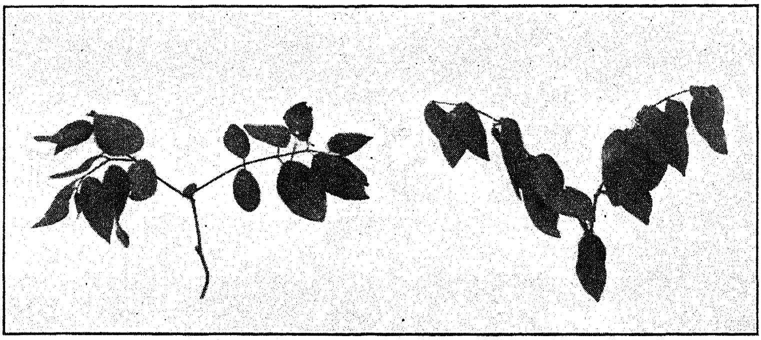

FIG. 195.—Plants of the dogbane (*Apocynum androsæmifolium*). The horizontal position of the leaves at night or early morning changes toward midday to the vertical, thus protecting the leaves from the direct rays of the sun as well as from the strong radiation from the soil.

turning of the crown tends to maintain the leaves in a position at right angles to the rays. In the case of plants that grow in mats, a very common form in xeric habitats, the aggregation of stems brings about the protection of the leaves. In addition, mat-plants often have erect or oblique leaves.

Decrease through Rolling or Folding of the Leaf.—In a large number of plants, the amount of leaf surface exposed to dry air is reduced by the rolling or folding of the leaf (Figs. 195 and 196). In many leguminous plants, lack of sufficient water causes the leaves to assume the folded position similar to that which usually occurs at night. In many plants, of which the xerophytic grasses are the outstanding example, rolling usually occurs merely as a temporary compensation. In the leaves of such plants

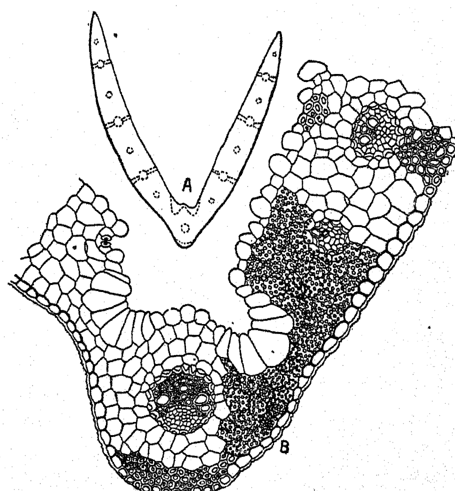

FIG. 196.—*A*. Diagram of a cross-section of a half-folded leaf of bluegrass (*Poa pratensis*) showing folding device and position of bundles and accompanying mechanical tissues. *B*. Detail of middle portion of leaf. During drought the large bulliform cells in the angles of the leaf in the upper epidermis become flaccid and cause the leaf to fold. When the water supply is increased they regain turgidity and the leaf opens.

the stomata usually occur more abundantly or entirely on the upper (ventral) surface. Hence, when the leaves roll inward, due to decreased

turgidity on the upper surface, or fold so that the edges touch, the stomata are well protected and the water loss is greatly reduced. The lower surface of the leaf is usually heavily cutinized. The furrowed leaves of monocotyledons, especially the grasses, are well adapted to changes of this nature. In addition to special motor cells on the upper surface, the T- and I-beams of mechanical tissues keep the leaf from collapsing and make it possible for it to roll.[205]

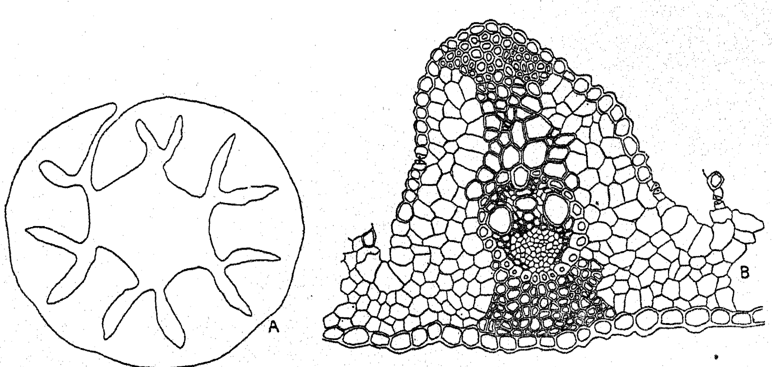

FIG. 197.—*A*. Outline of a rolled leaf of wheat grass (*Agropyron smithii*). *B*. Detail of one of the segments of the leaf showing bulliform cells of the rolling device on either side and the I-beam consisting of bundle and woody fibers which gives rigidity to the flaccid leaf.

The leaves of many xerophytic grasses and heath plants (*Ericaceæ*) are permanently rolled or folded (Fig. 197). The protection from drought is very effective, since the surface is reduced and the stomata lie in a chamber that is permanently and more or less completely closed. Many mosses roll and twist their leaves in consequence of drought, but in these the rolling merely reduces the leaf surface exposed. Among the club mosses, the rolling of the leafy branches into a compact ball, as in the resurrection plant, is an efficient protection against drought.

To Observe the Rolling and Folding of Leaves.—Detach leaves from various grasses and watch them fold or roll as they dry. Place the bases of dried plants of *Polytrichum commune* or other mosses with appressed or curled leaves in a little water and note the leaf movement as the water rises by capillarity among the leaves.

Decrease through Reduction of Leaf Surface or Loss of Leaves.—Plants reduce their surface and thereby the amount of transpiration by decreasing the number of leaves, by reducing the size of each leaf, or by changing its form. Among herbaceous plants, a decrease in size or a change in the shape of the stem brings about a similar result. In extreme cases of reduction, the leaves are completely lost (Fig. 198). Such a marked decrease in the amount of surface exposed is found only in extreme xerophytes, though it occurs in all deciduous trees and shrubs growing in

climates which are periodically dry, as a temporary adaptation to drought. The latter may result either from an actual deficiency of water, as in certain semitropical and tropical climates, or from its low availability due to frozen soil.

Changes in leaf form regularly produce a decrease of surface. The scale leaf, the linear or cylindrical leaf, and the thick, compact, succulent leaf are the most striking examples of reduced leaf form. Lobed or divided leaves usually show a tendency to reduce the size of the lobes or divisions when they are grown under drier conditions.

Changes of the Epidermal Cells.—Among the most common adaptations for decreasing water loss are heavy cuticularization and extreme cutin-

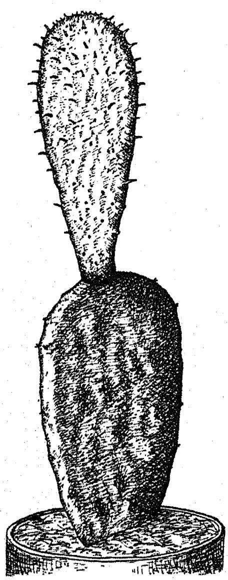

FIG. 198.

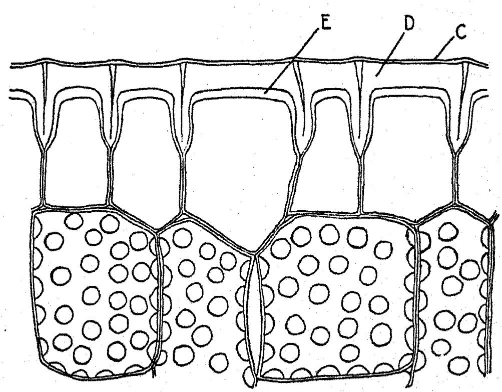

FIG. 199.

FIG. 198.—A cactus (*Opuntia*) showing deciduous, scale-like leaves on the young shoot. Although the shoot is only 4 weeks old, the leaves are beginning to fall.

FIG. 199.—Section from a leaf of *Aloe: C*, showing the cuticle; *D*, cutinized portion of the epidermal wall; and *E*, layer of cellulose. The first row of chlorenchyma is also shown.

ization of the epidermis. In some cases, the latter extends, also, to the subepidermal cells. All gradations occur from a cuticle slightly thicker than that in mesophytes to extreme cases where the cuticle is thicker than the diameter of the epidermal cells (Fig. 199). The cells of the epidermis are sometimes protected against evaporation by the secretion of a coating of wax, resin, or other material, or by the development of hairs (Fig. 200). Cuticle and wax may occur upon the same leaf, the latter forming a bluish-gray surface film, or a brittle crust, or layers of vertical rods, sometimes known as *bloom*. The formation of a hairy covering is usually precluded by either of these. Hairs often occur, however, on the lower side of a leaf that is cutinized above. The formation of a cuticle is the most perfect of all devices for decreasing permeability and thus reducing transpiration. In many desert plants,

the greatly thickened cuticle completely prevents all transpiration except that which occurs through the stomata. In these the cuticle is also developed in such a way as to protect the guard cells. Often, the air chambers below the stomata are lined with cuticle. Some species have a multiple epidermis, that is, one composed of two or more layers of cells (Fig. 201). While this is an effective protection against water loss, it is not frequent.

A coating of hairs screens the epidermis so that the amount of light and heat is greatly reduced and decreases the circulation of dry air over the leaf surface, preventing thereby rapid loss of water through the stomata. A few scattered hairs are of little or no value for this purpose, but a uniformly compact layer is of the greatest service, since it protects the stomatal openings as well as the epidermal cells.

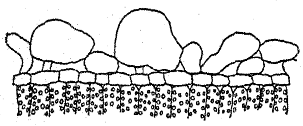

FIG. 200.—Portion of leaf of an orach (*Atriplex canescens*) showing the dense "meal" consisting of irregularly enlarged epidermal hairs.

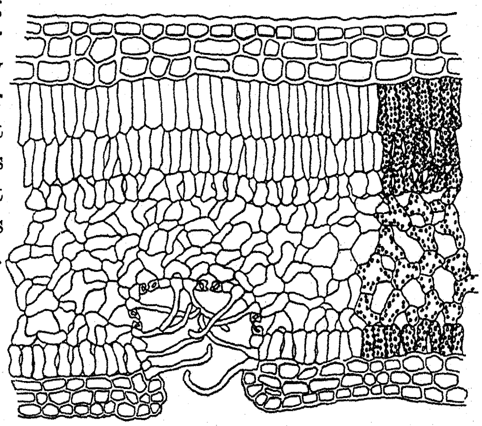

FIG. 201.—Leaf section of *Nerium oleander* showing the multiple epidermis and a section of the somewhat spherical stomatal chamber which is lined with simple hairs.

Such dense hairy coverings are found especially in species exposed to strong winds, as on plains and in alpine regions. Hairs are of the most various sizes and forms (Fig. 205). All hairy coverings have the same effect, which is to form a dead air space next to the epidermis where a relatively high humidity is maintained and the outward diffusion of water vapor from the leaf consequently reduced. The amount of radiant energy absorbed is also greatly decreased. The fact that they protect the stomata as well as the epidermal cells explains the efficiency of a hairy covering on the lower surface, even when it is absent from the more exposed upper side. In some cases hairs serve as screens to the stomata (Fig. 201). The efficiency of hairs in preventing water loss in wind-swept areas may be determined by their removal, whereupon transpiration is sometimes increased 25 to 50 per cent.[586] Until more experimental work is done, however, their efficiency in reducing water loss should not be over-emphasized.[444]

The epidermis is frequently modified to form reservoirs for the accumulation of water. These may consist of the epidermal cells proper, of

layers of water cells just beneath the epidermis, or of swollen cells found upon its surface.

Modifications of the Stomata.—Since stomata are the channels through which the great bulk of water loss ordinarily occurs, changes in these structures are of the utmost importance in reducing transpiration. Their modifications are many, but practically all of them are concerned with number and position. Where a species is subjected to increased drought, whether climatic or brought about by competition, the result is often a dwarfing of the plant and an increase in the number of stomata per unit area. The stomata develop early and if there is not enough water to cause the normal cell hydration and growth all of the leaf cells are dwarfed[61] (Fig. 202).

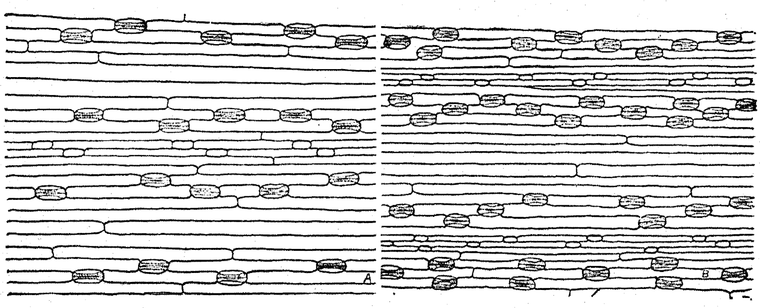

FIG. 202.—Unit areas of the epidermis of oats equally magnified. That with the fewer stomata and larger cells was grown under less xeric conditions.

Extensive investigations in England have shown that in general smaller leaves at any level on the plant have greater stomatal frequency than larger ones. There is a frequency gradient from the base to the apex of the plant, the higher leaves, regardless of size, having a greater number of stomata per unit area than the lower ones. This is closely influenced by the water relation as is shown by the fact that no such gradation develops in plants grown in a very humid atmosphere. The frequency of stomata, moreover, is not constant over the entire area of even a single leaf, but certain well-marked tendencies of distribution are evident. In dicotyledons, there is a frequency gradient from the base to the apex of the individual leaf and from the midrib to the periphery. This seems clearly related to distance from the water supply, cells at the base and near the midrib having the greatest supply and attaining the greatest growth. The stomata are consequently fewest per unit area in these portions of the leaves.[427]

A study of the woodland flora showed that the shrub layer had a greater stomatal frequency than the more mesic herbaceous one and that the tree layer, which is exposed to greatest desiccation, had the greatest number per unit area of all. Likewise, the flora at the margin of the

forest showed a greater stomatal frequency than the protected one beneath the forest canopy.

Similar relations have been found for the smaller cereals as a consequence of climatic drought; the number of stomata in barley, for example, increased progressively from 65 to 91 per square millimeter. In case of drought due to competition, a progressive increase in the number of stomata has been found in sunflowers planted in various densities in the same field. The plants ranged from 64 to 4 inches apart. The increase in the number of stomata per unit area is directly correlated with a decrease in their size.

TABLE 9.—STOMATAL CHARACTERS IN RELATION TO DENSITY OF PLANTING

Distance between plants, inches	64	32	16	8	4
Average number of stomata per square millimeter....	295	411	411	427	455
Average length of guard cells, microns..............	27	26	24	19	18
Average width of guard cells, microns..............	16	16	15	14	13
Average number of chloroplasts per stoma...........	23	21	20	19	15

Stomata of sun leaves are smaller than those of shade leaves and those of plants growing in dry habitats are smaller than those of plants growing in moist ones. Stomatal frequency can not be regarded merely as a means of adaptational adjustment with respect to transpiration, since the number of stomata per unit area increases as conditions for water loss become more severe.

In general, stomata are usually more numerous on the less exposed or lower surface of the leaf. In nearly all trees and in many shrubs, they are confined to the lower side. Exceptions occur in many shade plants where the exposure on the two surfaces is equal, and in aquatic plants in which excessive water loss is not harmful. The change in the number of stomata is well illustrated by a buttercup (*Ranunculus sceleratus*). When grown in water with the leaves floating, no stomata develop on the lower surface but in only moderately moist soil 40 per cent occurred on the lower surface.

Where plants grow under conditions of intense drought, the guard cells are usually found sunken below the epidermis, either singly or in groups. Sunken stomata are generally found at the bottom of chimney-like openings which may open below into more or less spherical cavities, the entrance sometimes being almost completely closed. When the stomata are sunken in groups, the cavities are commonly filled with protective hairs or the entrance closed by them. In both cases, the protection is very effective. The guard cells are screened from the intense insolation and from the dry air. The influence of dry winds is likewise almost wholly eliminated. This is true in a lesser degree for

stomata that are arranged in furrows protected by intervening ridges (Fig. 197). The cuticle often forms valve-like projections upon the guard cells or above them, and these serve to reduce the size of the openings. In some cases, moreover, the size of the pore formed by the two guard cells is permanently reduced. In a few plants, the effect of intense drought is almost completely prevented by closing the pore by means of a waxy secretion.

Changes in Chlorenchyma.—The rapidity with which water escapes from the tissue of the leaf is largely determined by the size and number of the air passages. Water vapor reaches the stomata most easily when the air passages are large and continuous and least readily when they are small and scattered. Consequently, leaves exposed to the danger of excessive water loss usually have a compact tissue in which the size of the air space is reduced and especially the size of the passages that connect them with the pores of the stomata. An increase of palisade tissue markedly decreases many of the air spaces and thereby greatly reduces the amount of transpiration.

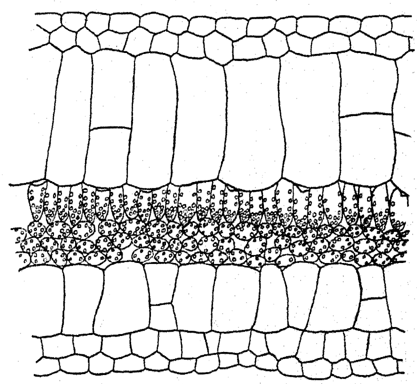

FIG. 203.—Cross-section of a leaf of begonia. The multiple epidermis represents a peripheral water-storage tissue. In the funnel-shaped palisade cells the chloroplasts are grouped chiefly at the lower end.

As an additional protection against water loss, many plants possess one or more layers of special cells immediately beneath the epidermis. Such hypodermal structures are common in mesophytic stems where they furnish increased support; when present in leaves, they also add rigidity. In leaves they consist of layers or masses of greatly lignified fibers or merely cutinized cells similar to those of the epidermis. In a few cases the walls of the palisade cells are partly lignified. Gums and tannins are of frequent occurrence in this layer. Beneath the epidermis or hypodermis there often occur in xeric leaves masses of sclerenchyma fibers or stone cells occupying space that in mesophytes is given over to chlorenchyma. These occur either as a continuous sheet or as groups of cells. They may act as a partial screen against intense insolation and thus reduce water loss, while at the same time they furnish support to the leaf.

Many xerophytes have become adapted to a decreased water supply by the change of part of the chlorenchyma of the leaves into cells where water or mucilaginous substances accumulate. In its extreme expression, such plants have succulent or fleshy leaves or stems. Otherwise, they

may have few adaptations for preventing water loss. Storage devices occur chiefly in the leaves, where they are of great importance. They increase the water supply by storing the surplus absorbed water which is used during drought. If peripheral, the water-storage tissue may also serve to protect the underlying tissues against excessive light. They often retain the stored water with great tenacity and thus tend to offset the forces causing evaporation (Fig. 203).

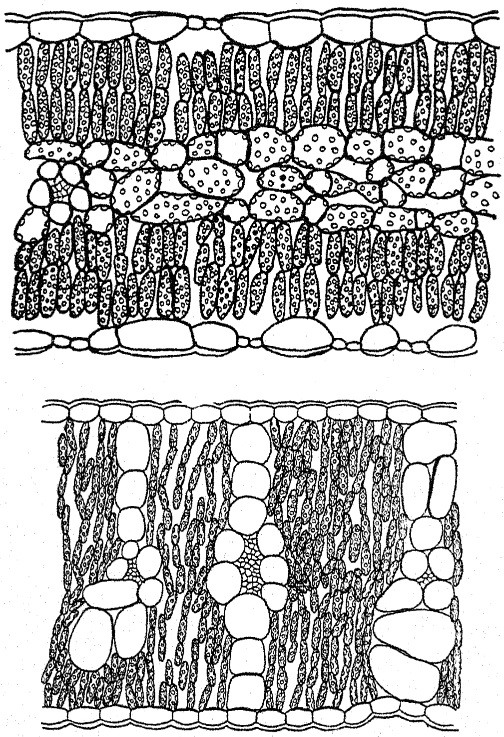

FIG. 204.—Cross-section of two types of storage leaves. The storage layers are transverse in forget-me-not (*Mertensia linearis*), and vertical in the gum weed (*Grindelia squarrosa*).

Water cells of the chlorenchyma may be scattered singly or arranged in groups. The groups of water cells are sometimes scattered but they usually occur in transverse bands or in horizontal layers (Fig. 204). Such layers usually lie between the palisade and sponge tissues and connect the bundles. A few plants possess tracheid-like cells that serve to store water. In the case of succulent leaves, practically the whole chlorenchyma is used for storing water. Such leaves retain their water tenaciously by virtue of pentosans, mucilages, etc. This is well shown when an attempt is made to dry them. Russian thistles (*Salsola pestifer*), for example, remain alive for many days after being detached from

the soil. Cells of water-storage tissue are usually thin walled, but the walls are frequently reinforced to prevent collapse when turgor is reduced.

Types of Leaf Xerophytes.—The organ that is most strikingly modified in xerophytes is the leaf. When the leaves are greatly reduced or absent, the stem is usually most modified. Leaves exhibit a large number of variations in size, form, texture, and structure. Several of these are often combined in one leaf, though, as a rule, one alone is well developed. The most satisfactory grouping of xerophytes is upon the basis of the leaf, since it is the organ most directly affected. Hence, those plants on which the leaves are present and properly modified may be termed leaf xerophytes.

In leaf xerophytes, adaptation has acted primarily upon the leaf, while the stem has remained normal or has changed but slightly in most instances. In some cases, the leaves have been reduced to scales, but even then they persist throughout the growing season and continue to take the primary part in photosynthesis. Leaf xerophytes may be arranged in groups based upon the form of the leaf or its structure. Since the same leaf sometimes shows two or more structural modifications, a grouping with respect to form is the most satisfactory. The following types may be distinguished:

Normal Leaf Xerophytes.—The leaf is normal in size and shape and of the usual dorsiventral character. The necessary decrease in transpiration is brought about by structural modifications rather than by a reduction in size. Three well-defined subtypes may be recognized with respect to the structure that prevents excessive transpiration. These are the cutinized, the lanate or hairy, and the storage leaf.

Cutinized Leaves.—This type compensates drought by thickening the outer wall of the epidermis and rendering it impervious by the addition of cuticle. The cuticle thus formed sometimes becomes very thick and the cutinized wall may fill half or more of the cell cavity. It is usually thicker upon the upper surface of horizontal leaves but is more uniformly developed upon upright or oblique ones. It is often reinforced by a marked development of palisade tissue. Practically all xerophytes with smooth leaves belong here, though many of them have storage cells as well. Cutinized leaves are usually leathery in texture, *e.g.* four-o'clock (*Allionia*), beardtongue (*Pentstemon*), and, in addition, they are often evergreen.

Leaves that are normal in size and shape but evergreen and so highly cutinized that they are hard and stiff are termed *broad-leaved sclerophylls.*[112] Live oaks, olives, oleanders, rubber plants (*Ficus elastica*), and many low ericaceous herbs and shrubs such as twinflower (*Linnaea*) and bearberry (*Arctostaphylos*) are representative. In addition to reducing water loss, the thick cuticle affords protection against mechanical injury by wind, insects, and grazing or browsing animals and also

from invasion by fungi. The leaves may likewise show other xeric structures.

To Examine the Structure of Cutinized Leaves.—Examine specimens of a number of the preceding species. Cut cross-sections and note the thickness of the cuticle. Examine both freshly cut sections and prepared slides of the rubber plant (*Ficus elastica*) or oleander (*Nerium oleander*). Draw a narrow segment of one, showing in detail the thickness of the cuticle, the three-layered epidermis, the double or triple row of palisade cells, the well-developed sponge region, and the sunken stomatal chambers on the lower surface. In *Ficus*, each chamber contains a single stoma; in *Nerium*, there are many in the hair-lined cavity. Add a drop of hydrochloric acid to the freshly cut sections of *Ficus* and note the effervescence of the pendulous concretions of calcium carbonate (cystoliths) in the upper epidermis.

Storage Leaves.—This type is distinguished by the water-storage cells or tissues developed in the chlorenchyma. It usually shows a well-developed cuticle, with several rows of palisade tissue, and may consequently be regarded as a special modification of the cutinized leaf. The storage cells retain a reserve supply of water, which is slowly yielded to the other cells in times of extreme drought. They differ from the cells of the palisade or sponge in size and shape but their origin from these is indicated by the fact that in some species chloroplasts are still present, though reduced in number (Fig. 204). Xerophytic species of *Mertensia* and *Erigeron* illustrate the more frequent arrangement in which the water tissue forms horizontal layers, while certain species of *Helianthus*, *Grindelia*, *Psoralea*, etc., have their tissues disposed in transverse bundles or rows.

A Study of Storage Leaves.—Examine cross-sections of leaves showing both types of arrangement of water-storage cells. Note especially the extent to which chloroplasts are represented in the water-storage cells. Do the leaves show any other xeric characters?

Lanate Leaves.—These are leaves with dense, hairy coverings on one or both surfaces. Hairs are usually stiff, thick-walled, epidermal outgrowths, which are often dead and filled with air at maturity. Types of hairs are numerous. They may be long and simple as in the velvet leaf (*Abutilon*), certain vervains (*Verbena*), and cinquefoils (*Potentilla*); appressed or matted as in cat's-foot (*Antennaria*) and silver poplar (*Populus alba*), etc.; stellate or otherwise branched as in mullein (*Verbascum thapsus*) and many crucifers and mallows; or scale-like or peltate as in the silverberry (*Elæagnus*) and buffalo berry (*Shepherdia*) (Fig. 205). Like cuticle and resin, hairs are common on bud scales as well as on leaves. An epidermis covered with a dense layer of hairs regularly lacks a well-developed cuticle. The protection against water loss, moreover, is so perfect and the light is so greatly reduced that the chlorenchyma often assumes the loose structure found in shade leaves.

A very large number of plants obtain their protection against drought by means of hairs. Indeed, they often give a characteristic grayish aspect to the vegetation as in sagebrush deserts. In a few cases, hairs are confined to the upper surface, and in many, to the stomata-bearing lower side, but as a rule they are nearly or quite as abundant upon both surfaces of the leaves.

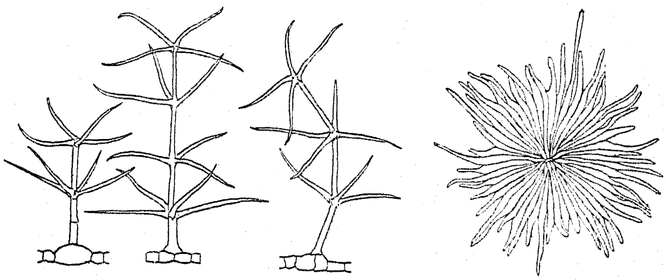

FIG. 205. –Compound hairs of mullein (*Verbascum thapsus*), and a top view of the multicellular, shield-shaped, scale hair of the silverberry (*Elaeagnus*) which is attached to the epidermis by a short stalk.

To Examine the Structure of Lanate Leaves.—Examine under the binocular microscope representative leaves (herbarium specimens will suffice if fresh material is unavailable) showing each of the above types. Examine freshly cut or prepared sections of mullein or other densely hairy xerophytes, and note the absence of well-developed cuticle and the very loose structure of the chlorenchyma.

Other Leaf Xerophytes.—Many species have lost the normal form of the leaf in response to dryness. In all cases, the reduction of leaf surface in proportion to volume is the characteristic feature, a result that has been attained sometimes by thickening of the leaf, by lobing, by rolling, etc. In addition to a reduction of surface, such leaves often have a thick cuticle, a hairy covering, or storage tissue.

1. The Succulent Form.—Many succulent leaves are normal in shape and size, though they are always thicker than ordinary leaves, as in begonia and purslane. Usually, however, they are reduced in size and more or less cylindrical in form (Fig. 114). The necessary decrease in transpiration is secured by reducing the surface and by storing water. The epidermis is often covered with a waxy coat, as in live-for-ever (*Sedum*), and, in addition, may possess a very thick cuticle, as in the century plant (*Agave*). Most succulent plants, however, exhibit weak cutinization. Most fleshy species, including especially those of alkali areas, have a cell sap of high osmotic concentration. Pressures of 30 to 80 atmospheres are not uncommon as compared to 10 to 25 for ordinary mesophytes and 3 to 5 for hydrophytes. On the other hand, certain fleshy plants, notably the cacti, yield relatively low pressures. An abundance of mucilages, gums, and pentosans in many succulents aid in holding the water against the forces of evaporation.[137]

Internally the tissues are quite compact. While in some cases all of the cells may contain chloroplasts, though usually less abundant in those near the center, more often there is a differentiation between chlorenchyma and water-storage tissue (Fig. 206). The chlorenchyma is usually peripheral, the outermost part sometimes palisaded, and the interior of the leaf consists of more or less isodiametric water-storage cells. In some cases, *e.g.* begonia, the water-storage tissue consists of a multiple epidermis, and the centrally placed chlorenchyma is well protected from strong insolation and water loss. Such succulent xerophytes as greasewood (*Sarcobatus*), sea blite (*Dondia*), etc., are able to grow in extremely dry alkaline deserts.

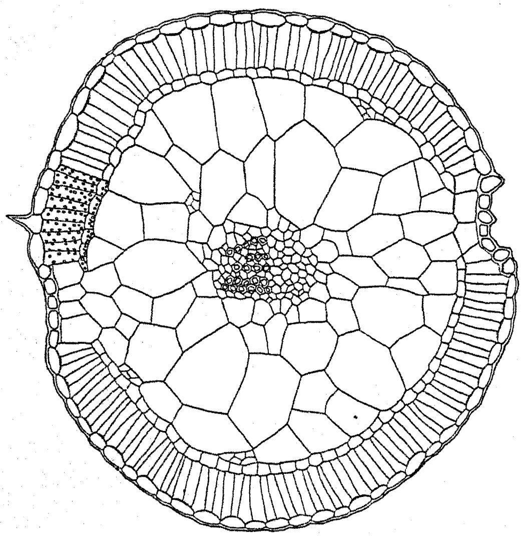

FIG. 206.—Section of leaf of the Russian thistle (*Salsola pestifer*) showing the large amount of water-storage tissue.

A Study of Succulent Leaves.—Examine the leaves of Russian thistle (*Salsola pestifer*), century plant (*Agave*), and live-for-ever (*Sedum*) or houseleek (*Sempervivum*). Draw a thin segment of one type. In *Salsola* note the sharp differentiation between chlorenchyma and water-storage tissue. In fresh leaves of the century plant, make out the peculiar epidermal characters consisting of wax grains, cuticle, cuticular layer, and cellulose layer of the epidermal walls. Note the extent of palisade and depth to which chloroplasts occur. Compare the rate of wilting in an excised leaf of begonia with that of sunflower, bean, or other mesophyte.

FIG. 207.—Dissected leaf of a wormwood (*Artemisia canadensis*), a gilia (*Gilia aggregata*), and a ragwort (*Senecio riddellii*).

2. The Dissected Form.—In these, the reduction of surface is brought about by the division of the leaf blade into narrow linear or thread-like lobes which are widely separated. The resulting decrease in exposed surface is considerable, in some cases exceeding nine-tenths of the gross outline. The lobes or segments are themselves protected by a hairy covering or a thick cuticle, which is often supplemented by many rows of palisade tissue or by storage tissue. *Artemisia,*

Gilia, and *Senecio* contain xeric species that are good examples of this type (Fig. 207).

A Study of Dissected Leaves.—The student should familiarize himself with this type of leaf xerophyte by an examination of representative specimens either in the field or in the herbarium.

3. The Grass Form.—Xeric grasses and sedges have narrow, filamentous leaves with longitudinal furrows which serve to protect the stomata. The furrows are sometimes filled with hairs as an additional protection, and the leaves often further reduce their surface by rolling inward when exposed to desiccation. They also contain a large amount of sclerenchyma which renders water loss difficult. The elongated awl-shaped leaves of *Juncus* and certain *Cyperaceæ* are essentially of the grass type, though they are usually not furrowed.

A grass leaf consists essentially of a series of parallel bundles, varying chiefly in size and amount of mechanical and conducting tissue, between which chlorenchyma is supported (Fig. 208). Immediately surrounding the bundle is a sheath of cells often with much thickened, lignified walls. Commonly there occurs a second layer of thin-walled parenchyma cells, either with or without chlorophyll. Strands of sclerenchyma tissue ordinarily accompany the bundles and frequently form with the larger ones I- or T-beams of mechanical tissue extending across the leaf. The epidermis, especially the lower or dorsal one, is highly cutinized. Over the vascular bundles the epidermal cells are often smaller and thickwalled, while bulliform (motor) cells, usually greatly enlarged, occur on the ventral surface between the larger veins. Frequently, they lie at the bottom of well defined grooves or occupy the entire thickness of the leaf. They are thin walled, and when they lose their turgidity through desiccation, the leaf rolls upward and inward. Thus, the stomata, which usually occur in rows and nearly always only in the depressions of the ventral surface in the most xeric species, are well protected from water loss. Mechanical tissue is very effective in preventing the collapse of the leaf and permitting it to roll. The remainder of the leaf is given over to chlorenchyma, except in cases of extreme xerophytes where water storage tissue occurs. The tissue is compactly arranged, the chlorenchyma cells being either nearly isodiametric or somewhat elongated.

A Study of the Mechanism of Rolling.—Examine with a binocular microscope the upper and lower surfaces of wheat grass (*Agropyron*), needle grass (*Stipa*), or June grass (*Kœleria*). Detach a leaf and follow the process of rolling as it dries. Examine freshly cut sections of any of the above and also of *Bouteloua* or *Bulbilis*. Note especially the amount of tissue not concerned in photosynthesis. Make a list of the ways in which the species in Fig. 208 have become adapted to an increasing degree of xerophytism.

4. The Needle Form.—This is the typical leaf of pines, spruces, and other conifers.[302] Some species, *e.g.* piñon and yellow pine, grow regu-

larly in habitats of low water content, but in most cases the great reduction of leaf surface is an adaptation made necessary by the persistence of the leaves during winter and possibly, in part, to an inferior (tracheid)

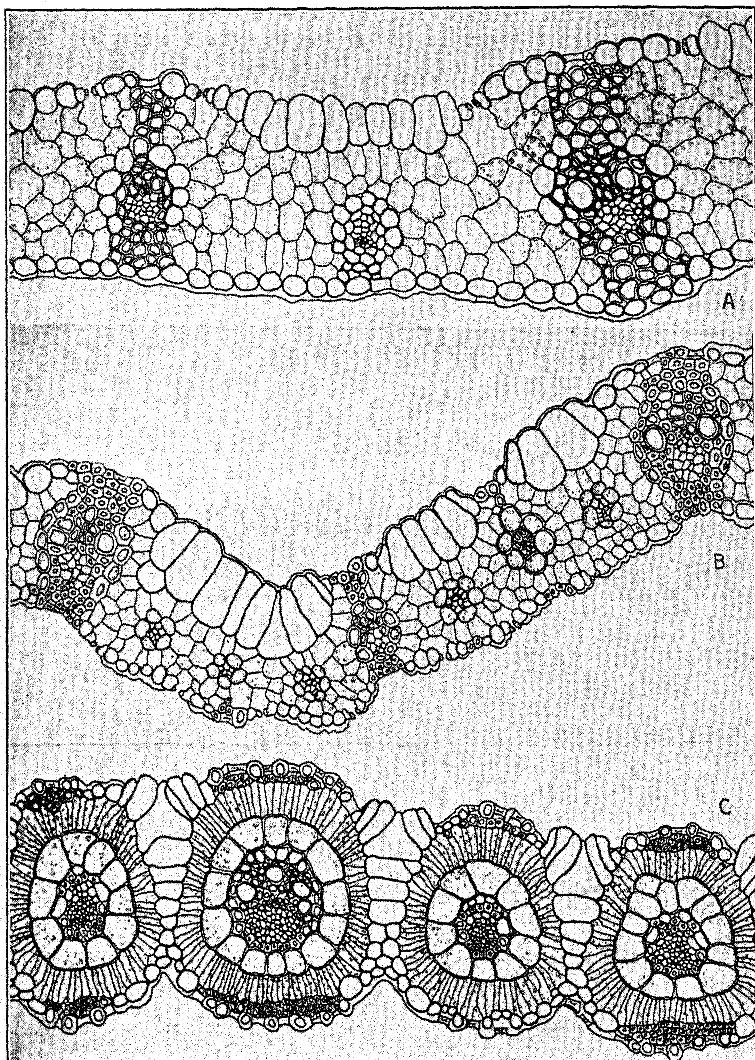

FIG. 208.—Cross-sections of the leaves of three grasses; (*A*) nodding wild rye (*Elymus canadensis*) is less xeric than (*B*) little bluestem (*Andropogon scoparius*); (*C*) blue grama (*Bouteloua gracilis*) is most xeric of all.

type of conducting system.[198,516] The leaves continue to transpire at a time when the available water is low on account of freezing. The relatively small water loss from the leaves is further decreased by a thick

cuticle, sunken stomata, and often by layers of sclerenchyma just below the epidermis (Fig. 209). When the stomata are closed, the leaf is almost hermetically sealed. Experiments with various species of conifers have shown that the water loss from the leafy shoots is no greater in winter, area for area, than that of the twigs of deciduous trees.[258,573]

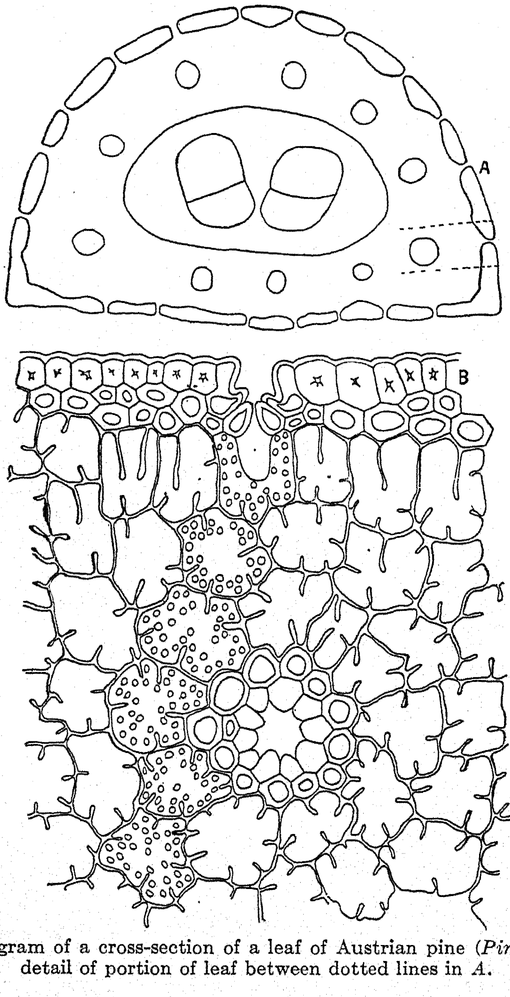

FIG. 209.—A, diagram of a cross-section of a leaf of Austrian pine (*Pinus austriaca*). *B*, detail of portion of leaf between dotted lines in *A*.

To Examine the Structure of Needle Leaves.—The characteristic structures are well shown in the Austrian pine (*Pinus austriaca*). Cut through the tough outer part and strip it from the leaf. Examine under low power the long, frayed, colorless, fiber-like epidermal cells and rows of sunken stomata. Examine thin cross-sections of the living leaf and also prepared slides. Make a very large outline of the whole leaf showing its various regions and, using high-power magnification, fill in a small amount of each kind of tissue. Note that the epidermal cells are highly cutinized and that the walls are so much thickened with lignified materials that the lumina are nearly

occluded. The rigidity of the leaf is due to the epidermis and the hypodermal layers of elongated sclerenchyma cells. The mesophyll, which is uniform throughout except for areas occupied by resin ducts, is characterized by peculiar plate-like infoldings of the walls. The single, central bundle region is invested by a sheath and traversed by two parallel bundles. The remaining tissue within the sheath is the so-called transfusion tissue. It consists of two kinds of parenchyma cells, those without protoplasm and pitted, and those with protoplasm and not pitted. The former may represent in function an extension of the tracheid system, passing water from the xylem to the mesophyll, and the latter cells are said to mediate between the mesophyll and phloem in the transfer of food.

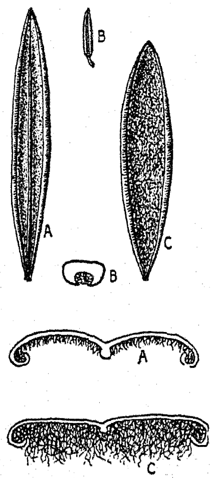

Fig. 210.

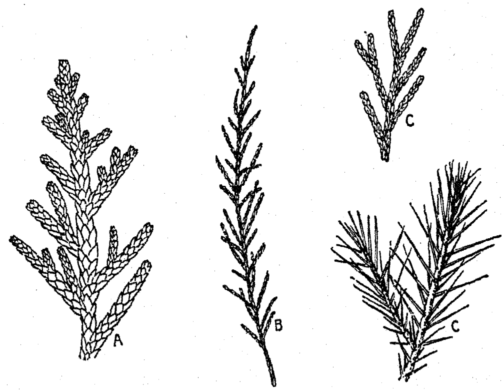

Fig. 211.

Fig. 210.—Under surface and outlines of cross-sections of three ericads; (*A*) bog rosemary (*Andromeda glaucophylla*), (*B*) a heath (*Erica*), and (*C*) Labrador tea (*Ledum groenlandicum*).

Fig. 211.—Scale leaves: *A*, of arborvitæ (*Thuja occidentalis*); *B*, tamarisk (*Tamarix gallica*); and *C*, variation from the scale form to awl-like leaves in red cedar (*Juniperus virginiana*).

5. The Roll Form.—Roll leaves are frequently small and linear. Their characteristic form is produced by the rolling in of the margins on the underside. This forms a more or less completely closed chamber for the protection of the stomata, which are regularly confined to the lower surface of the leaf. The upper epidermis has a thick cuticle and the lower one is often covered with hairs. The roll type is found especially among genera of the *Ericales*, but it also occurs in a number of other families (Fig. 210).

A Study of the Roll-leaf Form.—Examine specimens of bog rosemary (*Andromeda*), Labrador tea (*Ledum*), and heather (*Calluna*).

6. The Scale Form.—The reduction to a scale represents the extreme modification of the leaf under xeric conditions.[188] The next step results in the loss of the leaf and the assumption of its functions by the stem. Scale leaves are short and broad, leathery in texture, and closely appressed

to the stem as well as often overlapping. They are characteristic of many trees and shrubs, especially gymnosperms, such as arborvitæ (*Thuja*), cypress (*Cupressus*), junipers (*Juniperus*), tamarisk (*Tamarix*), etc. (Fig. 211).

Stem Xerophytes.—Stem xerophytes are characterized by the absence of leaves. In some plants, the leaves are present at first but fall early in the season (Fig. 198). In many cases, the leaves are reduced to functionless scales or are entirely absent. The functions of the leaves are transferred to the stems, which assume many of the structural modifications of the former. The stem or some part of it often becomes so

FIG. 212.—Phyllodes of two species of *Acacia* about one half natural size.

changed that it is readily mistaken for a leaf, as in the smilax of the florist. A number of types of stem xerophytes have been recognized, although not all plants of these types are now xerophytes.

1. The *phyllode* or bladeless leaf form consists of a petiole (stem) broadened into a leaf-like structure. It replaces the leaf blade which is entirely lacking. Such structures are common in many Australian acacias (Fig. 212). Most of these species have pinnately compound leaves in the seedling stage, but they soon give way to the simple phyllodes. It seems certain that xerophytes originated from mesophytes, and the presence of leaves in the juvenile stage of many xeric species is significant.

2. In the *virgate* or rod form, the leaves are either small and few or reduced to functionless scales or fall early. The joint fir (*Ephedra*), the twig bundle (*Lygodesmia*), scouring rushes (*Equisetum*), and certain

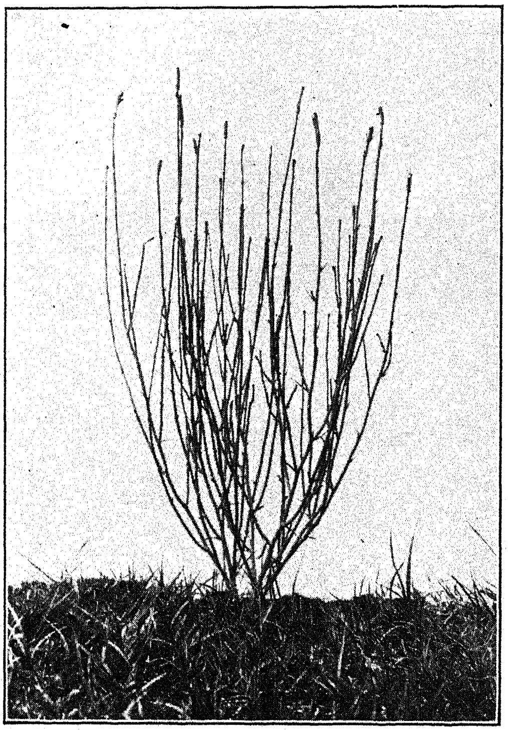

FIG. 213.—*Lygodesmia juncea* (Gr. twig bundle), a virgate or rod form of stem xerophyte.

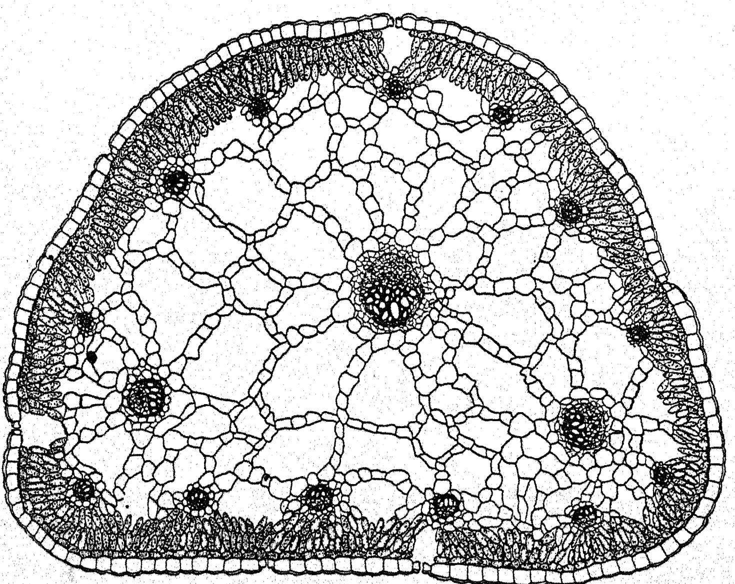

FIG. 214.—Cross-section of the stem of a rush (*Juncus balticus*). (*After Pool.*)

types of knotgrass (*Polygonum*) are representative (Fig. 213). The stems are thin, erect, and rod-like and are often greatly branched. They usually possess a thick cuticle and much palisade tissue, and the stomata are often sunken in longitudinal furrows.

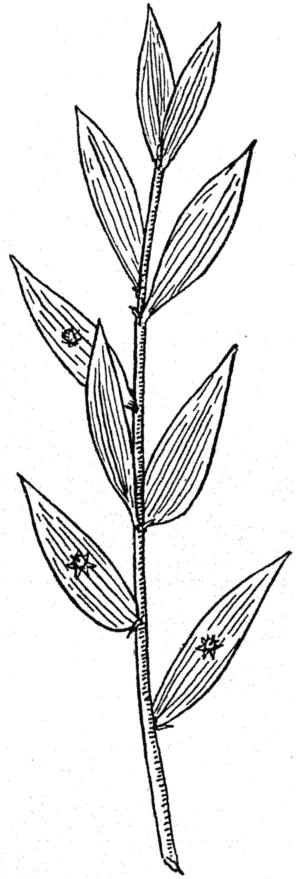

FIG. 215.—A small branch of butcher's broom (*Ruscus aculeatus*) showing the leaf-like cladophylls, some of which are bearing flowers.

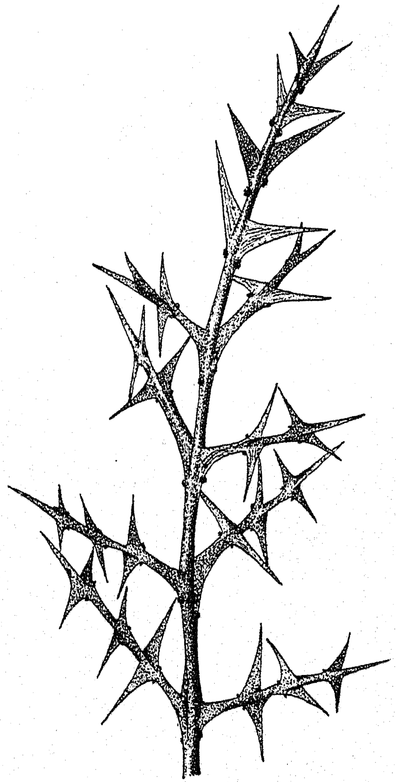

FIG. 216.—Branch of a thorn form of stem xerophyte (*Colletia*) about one-half natural size.

3. In the *rush* form, as represented by many species of rushes (*Juncus*), spike rushes (*Eleocharis*), sedges (*Scirpus*) and other *Cyperaceæ*, the stem is nearly or completely leafless, cylindrical, and unbranched (Fig. 40). It usually possesses a thick cuticle and several rows of dense palisade tissue. Most of these plants are not now xeric, as is indicated by the abundance of aerenchyma and high transpiration rate (Fig. 214). It is of great interest that leafless plants occur in such extreme habitats as swamps and deserts.

4. Another type of xerophytic stem is exhibited by *Asparagus.* Here the leaves are reduced to mere functionless scales, and their work is assumed by the small needle-shaped branches, *i.e. cladophylls* (or branch leaves). The cladophyll of butcher's-broom (*Ruscus*) is firm, hard, and spiny tipped and reveals its stem character by bearing flowers on the middle of one face (Fig. 215). In the smilax of the florists, which is really an asparagus (*A. asparagoides*), the cladophyll is wholly leaf-like in appearance as well as in function.

FIG. 217.—Papago Indian, near Torres, Mexico, drinking the water which he has squeezed from the tissue of a cactus (*Echinocactus*) into the cavity formerly occupied by the tissue. (*After Coville and MacDougal.*)

5. The *thorn* form of stem xerophytes is typical of many spiny desert shrubs in which the leaves are lost very early or are reduced to mere functionless scales. The stems have an extremely thick cuticle, and, as a rule, the stomata are sunken or protected by valves. *Colletia, Koeberlinia,* and *Holacantha* are good examples of this type (Fig. 216).

6. The *succulent* form is represented by plants with fleshy stems such as *Euphorbia, Stapelia,* and the *Cactaceæ.* They have decreased water loss by the extreme reduction or loss of leaves and by reducing the stem surface. In the cactus, for example, leaves are wanting except during the early stages of growth, and then they occur only as small scales at the

nodes. The stems may remain smooth and round or become fluted by the presence of vertical green ribs or become flattened in various degrees, but they are always thick and fleshy. Fluted stems, such as those of the giant cactus (*Carnegiea gigantea*), undergo accordion-like expansion and contraction during moist and dry periods, respectively.[330] The flattened types present a small amount of surface in proportion to the mass of contained tissue; the surface is further reduced in the thick, cylindrical type and reaches a minimum in the spherical form. In addition to a decrease in transpiring surface, they further reduce water loss by means of water-storage tissue with high colloidal content (pentosans, etc.). Growth is slow because of the small surface exposed to light, although the chlorophyll extends much deeper than in most stems and leaves, but some attain the proportion of trees and may have a reserve supply of many tons of water stored in the pulpy interior[330] (Fig. 217). Because of their xeric characters, which usually include a highly developed cuticle and sunken stomata, the plants lose water so slowly that they may continue to live for several years without an additional water supply. Thorns and spines are also more or less characteristic, though they serve only slightly and incidentally against water loss.

Form and Structure of Stem Xerophytes.—Draw carefully in outline and to scale the stem or shoot of a representative plant of each type. Make a drawing of a portion of a cross-section of a stem of the virgate or the rush form and compare it with the needle leaf. Transect the stem of a cactus and note especially the depth to which the chlorophyll extends, the mucilaginous cell substances, and the nature of the thick "rind" as regards cuticle, epidermis, sunken stomata, etc.

CHAPTER XVI

RELATIONS BETWEEN PLANTS AND ANIMALS

The primary relation between plants and animals is that of the food supply. This arises from the fact that plants manufacture practically all the food used by the world of organisms and in so doing provide most of the materials and shelter utilized by animals. A direct outcome of this is the necessary association of animals with plants in the same community, out of which springs a multitude of interactions. Plants constitute the permanent basis of the biotic community on land, not merely because they are stationary, but especially because of their direct relation to the environment or habitat. They are subjected to the immediate action of the latter, and, in turn, they exert a marked effect or reaction upon the habitat. By contrast, animals are much more dependent upon the food supply than upon the environment, and, hence, their most striking relations are with plants. These are termed *coactions* and together with the action of the habitat upon organisms and the reaction of the plants upon the habitat make up the three major processes of every community.

While the number of concrete coactions in any community is limited only by the number of species and individuals in it, these fall into but a few categories. From the standpoint of the organisms concerned, coactions may exist between plants, between plants and animals, and between animals. In the present instance, the concern is chiefly with those between plants and animals, where the universal relation is that of the food supply. Growing out of this is the coaction of shelter and of materials and a more general one of contact or disturbance, such as is seen in the trampling of herds or the carriage of fruits by attachment. Coactions may be mutually helpful, as in the case of pollination or the carriage of fleshy fruits, or they may be antagonistic or injurious to one of the organisms, as exemplified by grazing animals, parasitic insects, or bacteria.

POLLINATION

One of the universal coactions of plants and animals is that exhibited in pollination, *i.e.* the transfer of pollen from the anther to the stigma.[361a]

Significance and Methods.—The retention of the macrospore on the sporophyte, an advance characteristic of the flowering plants in contrast to the existing ferns and fernworts, made imperative some method of transferring the pollen grain or microspore. The open pistils of pines lent themselves to the transport of pollen by the wind, but the closed

pistils of true flowers seem to have been dependent upon insect pollination from the first, since nearly all simple flowers exhibit this method. In fact, this coaction is so fundamental and so completely reciprocal as to have had a large share in the evolution of both flowers and insects. Its importance, however, does not rest so much upon the structure of flowers as upon the nature of fertilization itself.

Since nearly all flowers with corolla possess both stamens and pistil, it would be expected that the pollen would fall directly from the anthers upon the stigma to produce pollination. This is so simple and yet so rare that it can be explained only by some fact of the first importance. The explanation was long ago supplied by Darwin,[135] who demonstrated by experiment that the best seeds and most vigorous offspring resulted from the transfer of pollen from one flower to another or, better still, from one plant to another. It is obvious that pollination takes place only by this method in all monœcious and diœcious plants, while in perfect flowers the same result is secured by having the anthers and stigmas mature at different times.

Arrangement of Stamens and Pistils.—Since the transfer of pollen from anther to stigma is imperative if fertilization is to ensue, the relative position and development of stamens and pistils become matters of great import. They not only affect the method of transfer but also determine the kind of fertilization that results. The arrangement by which stamens and pistils occur in different flowers is termed *diclinism*, and plants that possess staminate and pistillate flowers are said to be *diclinic*. Diclinic species are *monœcious* when the two kinds of flowers grow on the same plant and *diœcious* when the stamens are borne on one plant and the pistils on the other. When the stamens and pistils are found in the same flower, the flower is said to be *perfect* and the plant is termed *monoclinic*. The presence of perfect and imperfect flowers in the same species is called *polygamy*. In perfect flowers, the overwhelming rule is for anthers and stigmas to mature at different times, with the consequence that self-pollination is prevented, a condition that is termed *dichogamy*. Flowers of this type are called *protandrous* when the anthers shed their pollen before the stigmas become receptive and *protogynous* when the stigma matures first. When anthers and stigma ripen at the same time, the flower is said to be *homogamous*, but this condition is relatively rare.

Flowers regularly open before or upon the maturity of anthers or stigma, but sometimes they remain partly or completely closed to become *cleistogamous* and must then be self-pollinated. In homogamous flowers, self-pollination would be expected as a regular procedure, but the anthers and stigma are often so placed that this process is out of the question. In still other flowers, anthers and stigma stand at two or three different heights in relation to each other and the effective transfer of pollen is between members of the same level.[289]

Production of Pollen and Nectar.—The total amount of pollen produced by a species is determined by the number of flowers and stamens, and by the size of anther and pollen grain, as well as by the number of plants in a particular community. As a general rule, the amount of pollen produced increases with the danger of loss. Pollen grains are exposed to the double risk of injury by weather and loss in transit, especially in transfer by wind. Furthermore, they are often used for food by insect pollinators, and the number of grains actually transported may then be very small. Quantity production of pollen is attained in simple open flowers, such as those of the buttercup, anemone, and strawberry, by means of a large number of stamens, and this compensates for the heavy loss arising from the visits of pollen-seeking insects.

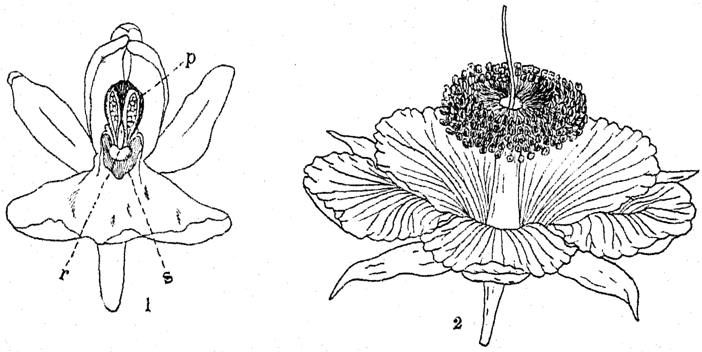

FIG. 218.—Extremes of pollen production. 1, an orchid (*Orchis*); *p*, pollen mass in anther cell; *r*, retinaculum; *s*, stigma. 2, a baobab flower (*Adansonia*) with a column of stamens. (1, *after LeMaout and Decaisne*; 2, *after Baillon*.)

Among the wind-pollinated plants the greatest loss occurs in the diœcious trees, such as cottonwood and ash, and such monœcious conifers as the firs, in which the pistillate cones are above the staminate ones. The need of compensation for loss under such conditions is very great and the amount of pollen required is enormous. In many trees, this waste of pollen is offset by the production of a vast number of small flowers, and especially of reduced ones in which the stamens have been emphasized at the expense of sepals, petals, and pistils. This process is still in operation in the various species of maples, which range from perfect flowers with all four parts to the greatly reduced ones of the diœcious box elder.[94]

In the case of insect-pollinated flowers, the number of stamens and, hence, the amount of pollen produced decreases as the method of pollination becomes more and more perfected, and also the number of flowers is often much reduced. Simple or primitive flowers may have several hundred stamens, but with increasing specialization of the flower for pollination the number drops to ten, five, and even one. In a large

number of irregular or zygomorphic flowers, the stamens are but four or two, and in the majority of the orchids but a single one (Fig. 218).

The production of nectar varies from species to species within limits almost as wide as those for pollen. While, however, the amount of pollen is fixed for each flower and, hence, to a large degree for the species concerned, the nectar flow fluctuates from season to season, day to day, and even hour to hour in some cases. It is directly influenced by the growing conditions for the season and often exhibits a distinct daily rhythm. This is so marked in such plants as the buckwheat that they are visited by bees only during the hours of the so-called *flow*. In many species, nectar is produced more or less constantly as long as it is removed. It accumulates when visitors are few or absent, but to very different degrees, depending upon the activity of the nectar glands, the size of the flower, and the nature of the plant. In some instances, the nectar is only a layer or droplet on a tiny nectar pad, while in others the nectary may consist of a long tube or spur with several cubic centimeters of nectar in it.

Protection of Pollen and Nectar.—The modifications that protect the pollen serve likewise for the nectar, though the latter may also be guarded by a special device of its own. In many instances, the protection afforded is secondary, the feature concerned having been developed primarily for other reasons, but the most striking devices serve directly for protection. The latter is exerted chiefly against the danger of wetting the pollen by rain or dew and the dilution of the nectar, though the nectar may also be guarded against marauders. Pollen is rarely if ever protected against loss or waste by visitors, since its free exposure promotes pollination and is offset by the large amount available.

The damage due to wetting is chiefly seen in the loading and transport of the pollen, though this may sometimes be injured by premature germination. Wind-pollinated species usually escape both handicaps, since the small flowers dry readily, as a rule, and the anthers are, for the most part, hung out for shedding during favorable weather. The extent to which bees are discouraged by dilute nectar is uncertain; at any rate, they return promptly as soon as the flowers are sufficiently dry to be profitably visited.

The devices that serve to protect pollen and nectar are of three kinds: (1) morphological, (2) mechanical, and (3) seasonal. The first and third seem to accomplish protection incidentally, while devices of the second type probably owe their existence to the necessity for protection. Morphological contrivances are purely structural or positional; to the first belong all those in which protection results from the structure or shape of the flower or its parts, or the flower cluster. Protection in consequence of the position of the flower or cluster occurs in a large

number of species in which the face is turned downward or the tubular corolla is horizontal or drooping (Fig. 219). Mechanical devices comprise movements of the flower or its parts, or of the inflorescence. In

FIG. 219.—Protection of pollen by the form and position of the flower in the bearberry (*Arctostaphylos uva-ursi*).

most cases, protection results from the closing of the corolla, more rarely from that of other flower parts or in composites from the movement of the ray flowers and bracts (Fig. 220). It may also be secured by the bending or drooping of the flower stalk or the stalk of the entire cluster.

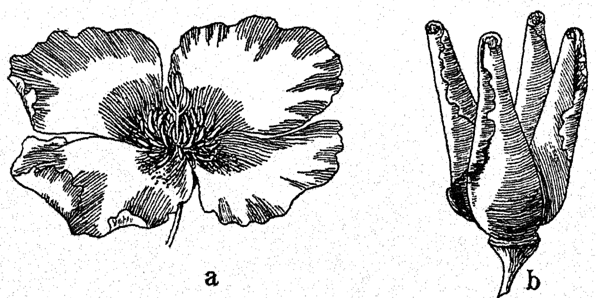

FIG. 220.—Protection of pollen in the California poppy (*Eschscholtzia californica*) by (*b*) the rolling of the petals in wet weather. (*After Kerner.*)

Movement is most rapid and conspicuous in day bloomers and night bloomers, while its value for protection is greatest in ephemeral flowers, which usually wilt and close a few hours after opening. Day blooming and night blooming bring about the effective protection of pollen during

the time when it is not being removed and may be injured, though the habit probably bears a more important relation to insect visits.

The Life History of a Flower.—All of the flowers of a plant exhibit the same behavior, which is characteristic of each species or often of the entire genus. This is made up of a round of changes that begin with the bud and continue their orderly progress until the fruit ripens or the seeds

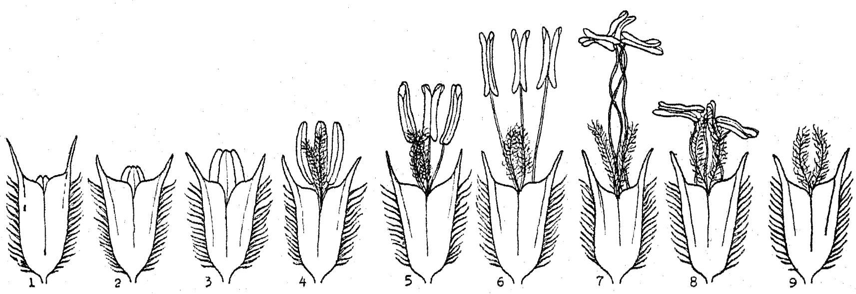

FIG. 221.—The pollination story of the timothy (*Phleum*).

are freed. Practically all of these are concerned with the details of the task of promoting cross-pollination or of securing self-pollination when needed and of protecting pollen and nectar. Such a round of life may consist of little more than opening the flower, shedding the pollen, and ripening the stigma, or it may embrace a score of changes and movements in which all the flower parts take a share. It stands in the most

FIG. 222.—The life history of a geranium flower (*Geranium*).

intimate relation to the actual work of pollination by insects and largely determines the number and effectiveness of the latter.

The life history of a wind-pollinated flower is simpler than that of those pollinated by insects, though it often comprises a number of stages, as is shown by timothy (Fig. 221). In the geranium (Fig. 222), it is more complicated, while the fireweed probably exhibits a maximum

number of stages (Fig. 223). In addition to the movement of the bud into the horizontal position and those of the maturing fruit, the group of stamens and the style uniformly pass through a regular sequence of changes. The minor details of the behavior may be modified by water and heat relations, rain and cold delaying the process or warm weather hastening it, with a corresponding effect upon the rate of development.[94]

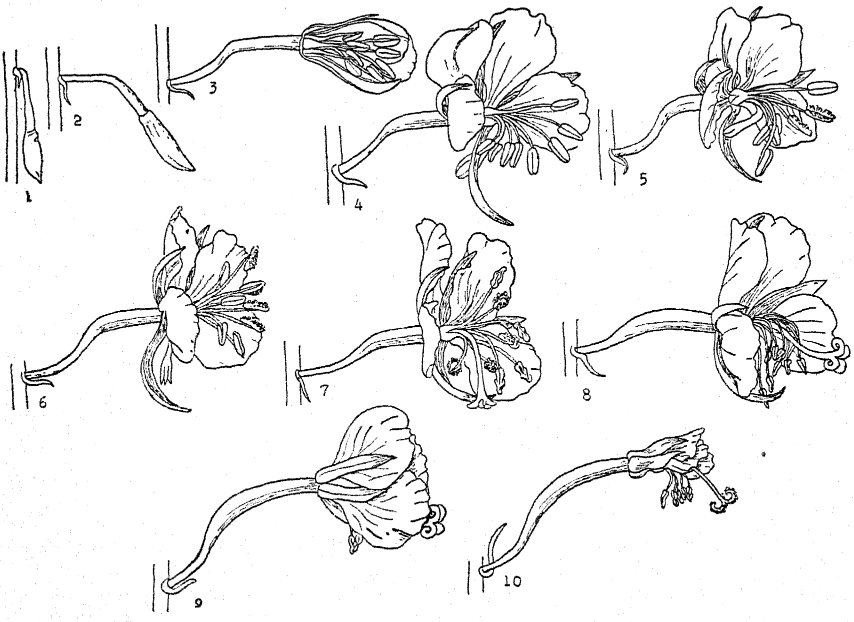

FIG. 223.—The pollination story of the fireweed (*Chamaenerion*).

The Round of Life of a Flower.—Label five well-developed buds of one plant by means of small tags and follow their development as far as the young fruit, recording the changes in growth and position and the behavior of the four parts at some time between 6 to 8 a.m., 12 to 2 p.m., and 5 to 7 p.m. This is usually best carried out by a cooperative group of students.

Kinds of Pollination.—When pollen is deposited on the stigma of the same flower, the latter is said to be self-pollinated, and the process is termed *autogamy*. If the transfer is from one flower to another, cross-pollination or *allogamy* takes place. Most species of perfect flowers are modified in such a way as to give a decisive preference to cross-pollination, but many of them may be self-pollinated when necessary. It is obvious that diclinic species, in which stamens and pistils are found in different flowers, are susceptible of cross-pollination alone. When anther and stigma are present in the same flower but ripen at different times, as in dichogamy, cross-pollination is an all but universal result and self-pollination is a rare occurrence. The latter is frequent, however, if not regular in homogamous flowers in which anthers and stigma mature simultane-

ously and can alone take place in all closed or cleistogamous ones. Self-pollination is the invariable rule in a relatively small number of plants which are apparently well adapted to the transfer of pollen, and such cases throw some doubt upon the accepted view that cross-pollination necessarily produces better offspring.

Many devices have been thought to insure self-pollination when allogamy fails for any reason, and careful observation shows that these do bring anther and stigma into contact in most instances. Their effectiveness, however, is usually small and often lacking, in consequence of the earlier removal of all the pollen or the drying of the stigma. Even when flowers are covered to prevent these consequences, it has been found that the setting of pods and production of good seeds is more or less exceptional, in native species at least.

Cross-pollination has been distinguished as *geitonogamy* when it concerns two flowers of the same plant and as *xenogamy* when the transfer is between different plants. The latter has been supposed to be more advantageous in the production of vigorous offspring, but this view needs further experimental test. It is a logical inference from the work of Darwin, which showed that cross-pollination yielded better results, and is likewise supported by the remarkable vigor of many hybrids. Hybridization itself results from the cross-pollination of two varieties or species and has yielded a myriad of new species and forms in field and garden. A special investigation to determine its rôle in nature indicates that it is rare, but this is a conclusion to be tested in many different floras.

Agents of Pollination.—Pollen is transported by animals, by wind, and by water. The latter is unimportant, since it concerns but a few submerged aquatics,[595] the great majority of hydrophytes being pollinated by the wind. In temperate and boreal climates especially, wind is the agent utilized by the large majority of trees and shrubs, by practically all grasses and sedges, and by many other herbaceous species with inconspicuous flowers. Wind-pollinated species regularly produce enormous amounts of pollen and possess some device for sifting this out on the wind, such as the hanging catkins of poplars and birches or the slender filaments of plantains and grasses. Styles and stigmas have been correspondingly modified for catching wind-borne pollen and have increased the receptive surface to the maximum, usually taking a bushy form but sometimes becoming long threads, like the "silk" of corn. This emphasis upon filament and stigma has been accompanied by the dwindling of the corolla, and, in consequence, most wind-pollinated flowers are small and inconspicuous.

Among animals, insects are the chief pollinators, though a similar rôle is assumed by humming birds, and, in the case of cultivated plants especially, man plays a significant part. Any insect that works in or

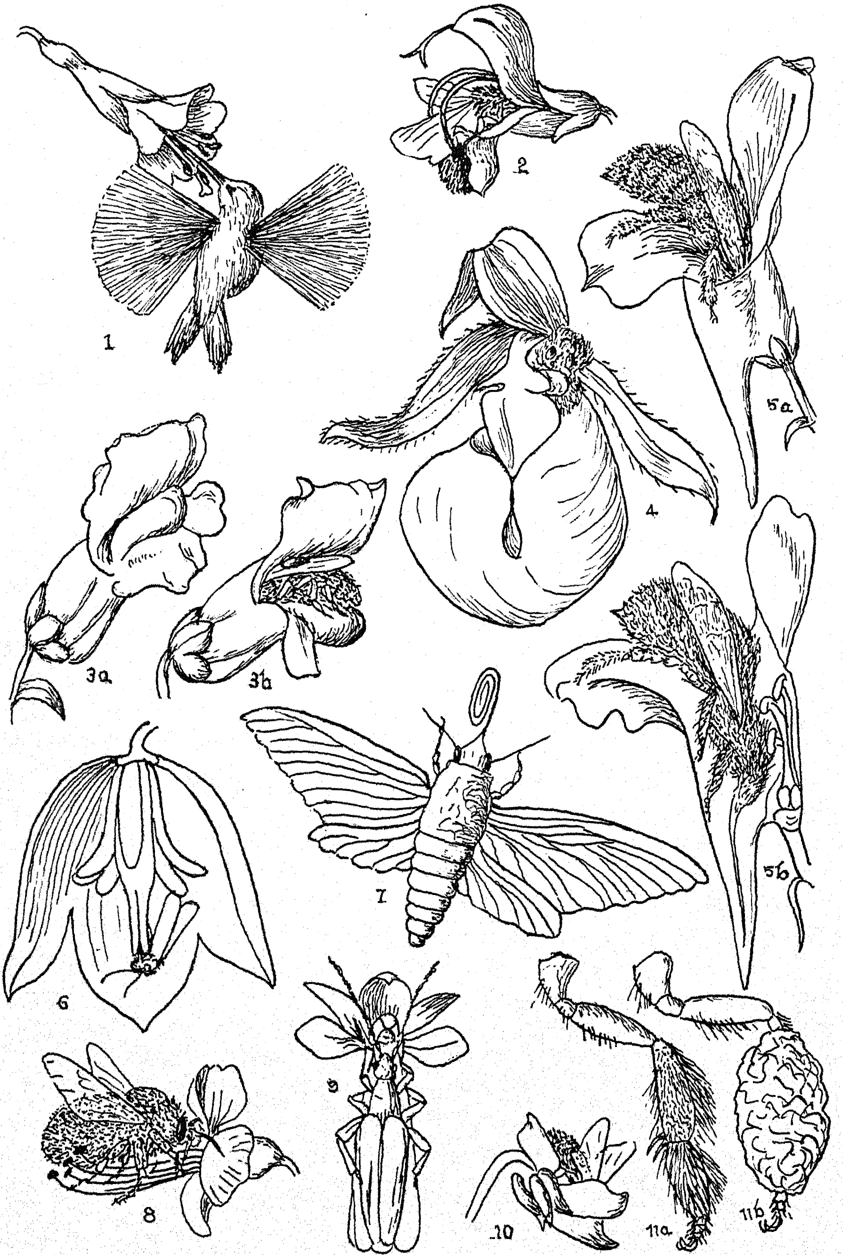

FIG. 224.—Flowers and their visitors. (1) Ruby-throated humming bird and humming-bird-trumpet; (2) blue sage pollinated by bee; (3) snapdragon; (4) bee escaping from pouch of lady's-slipper and rubbing against an anther; (5) butter-and-eggs; (6) yucca flower being pollinated by pronuba moth; (7) sphinx moth with long sucking tube; (8) bee on flower of horse-chestnut; (9) bettle on tway-blade; (10) honeybee in violet; (11) leg of bee with pollen basket: *a*, empty; *b*, loaded with pollen.

among flowers may become a pollinator, but as a regular activity, pollination is carried on by a few groups. The bees and their relatives are by far the most important,[323] followed by the butterflies and bee flies and at a much greater distance by the beetles. Bumblebees and honeybees are the most numerous and efficient, the honeybee outranking all other species in industry and intelligence.[233,380] For sheer efficiency the humming bird is probably without a peer among pollinators, but it is excelled by the bees in number and especially in the range of flowers visited. Orioles and other birds are known to visit flowers occasionally; some tropical flowers are pollinated by bats, and a few of the arums by snails (Fig. 224).

Attraction of Insects by Flowers.—It has long been recognized that insects are attracted to flowers by color, form, and odor as well as by nectar and pollen, but there has been much diversity of opinion as to the relative importance of the first three factors. It is difficult to discriminate between them by observation alone, when all three are present in the same flower, and consequently it becomes necessary to resort to experiment, by which each can be employed separately. A large number of experimental studies have been made during the past 50 years, and these have recently been compared and summarized in the light of a comprehensive investigation dealing with many species of flowers and insects in nature.[97] The conclusion has been reached that in the case of the honeybee the attraction exerted by color and form is about four times greater than that of odor, nectar, and pollen combined. It is possible that the influence of odor is somewhat greater in those flowers with a marked perfume.

In general, it seems to be well demonstrated that odor is the attractive feature for distances of more than 10 meters, color in mass for intermediate ones, and color and form in detail within 2 meters or so, depending greatly upon the size and color of the flower or cluster. For the majority of flowers without a marked fragrance, odor can be effective only near at hand. In the midst of a group of plants or of flowers, odor can exercise little influence. It is not only general in such instances, but it is also most powerful at the flower or cluster on which the insect is working. Such conditions do not permit it to go straightway and without hesitation to the next flower or head, and guidance by color and form alone can explain the assured and rapid flight of bees in the midst of flowers.

Since the senses of sight and smell differ greatly in the various groups of insects, the relative importance of the three attractive factors will be modified accordingly. On the basis of their behavior, bees have the best vision, followed in order by bee flies, butterflies, moths, and beetles. Because of the very different structure of the eye, humming birds evidently discern flowers at a distance of 100 yards or more and masses of bloom at much greater distances. On the other hand, it appears proba-

ble that fields of buckwheat, alfalfa, or mustard can be located by pollinators a mile or more away by the odor alone.

Experimental Pollination.—In the experimental study of the relation between flowers and insects, it is necessary to observe in detail the round of life of each flower and the behavior of the important pollinators that visit it. With this as a background it is possible to fashion a variety of experiments to determine the effect of color, form, and odor, the competition between insects for flowers and between flowers for visitors, the efficiency of different species, their learning capacity, power of memory and intelligence. Among the effective devices employed are the mutilation of flowers by reducing or removing parts, the addition of parts, artificial flowers, painting natural flowers in various colors, adding odor or nectar, masking odor or parts, and direct experiments with color, form, or odors. The efficiency of flowers in dusting bees with pollen, of the bees in transporting loads, and of flowers again in securing effective deposit on the stigma have all been studied experimentally.

Changes in the position of flower present new problems in landing to the visiting insect, especially in the case of inversion, but these are solved with more or less readiness, the time required depending chiefly upon the shape of the flower and the kind of visitor. The consequences of increasing the attractive surface of the corolla or of reducing it by mutilation are much more striking. Splitting the hood of monkshood (*Aconitum*) and turning the sepals back rendered such flowers more than four times as attractive as the normal ones. On the other hand, cutting away half of the corolla reduced its effectiveness to one-half or even to one-tenth in practically all cases and demonstrated the paramount importance of the corolla for attraction. When both lips were removed in the wild bergamot (*Monarda*), the number of visits was a twentieth of that for flowers with the upper lip removed and a tenth of that for those with the lower lip cut off. The removal of the petals in the geranium usually reduced the visits to zero, while cutting them to half their length diminished visitors in proportion.

Natural flowers painted with water colors have been found to be about five times as attractive as artificial flowers made of paper. The latter were visited about a fifth as often as the normal flowers, though much depends upon the closeness of the resemblance, some investigators obtaining abundant visits to them. In general, honeybees are more discriminating than bumblebees, though individual differences are considerable in both. As to colors, blue was regularly preferred to all others, red being the least attractive.[97]

Attraction and Guidance of Visitors.—In the case of regular flowers such as the geranium, remove the petals from several, cut them to half the normal length in an equal number, and employ the same number of unmutilated blossoms. Record the number of visits during a unit period to each and estimate the value of the corolla.

Cut off one or both lips of an irregular flower and note the effect upon the visiting insects. Place flowers in inverted or other unusual positions and note the behavior of the visitors.

Competition for Visitors.—Many suggestions as to the relative effectiveness of different species in terms of attraction can be obtained by observing the behavior of visitors to a mixed group, but experiment is indispensable to definite results. These can not be secured by placing the flowers of two or more species side by side, since bees, in particular, pay little attention to artificial groupings. In consequence, it is necessary to fasten an equal number of competing flowers on another plant and desirable, also, to make a similar reciprocal installation on the other species. This is due to the fact that the most intelligent species of pollinators have learned that they work most rapidly and effectively by devoting themselves exclusively or nearly so to the species with the greatest honey flow at the particular time. Young bees and very old ones are much less methodical than workers in their prime, and butterflies are even more easily turned aside in their quest. While installations for conclusive results require time and care, however, much information as to the habits of insect visitors and the attractiveness of different flowers can be obtained by placing bouquets of one species in the midst of the plants of another.

Competition for Insect Visitors.—Select a plant that is being abundantly visited and place among the flowers an equal number from a plant that differs conspicuously in the color, size, or structure of its flowers. Record the number of visits made to each species by the various kinds of visitors during a period of 10 to 30 minutes.

The degree of constancy shown by each pollinator can be determined by the composition of the pollen loads carried by bees, the pollen grains of the various flowers being readily recognized under the microscope. During the maximum period of flowering of the raspberry (*Rubus deliciosus*), the loads of 22 honeybees contained the pollen of this species alone; after this time the loads were obtained from six different species, but in all but one instance it was 99 per cent pure. In the case of bumblebees the constancy was less, but even here it was not less than 90 per cent as a rule.

SEED PRODUCTION AND DISTRIBUTION

In the production and distribution of seeds, animals usually play an important and often a controlling part. Hence, this is a coaction of primary importance in a study of vegetation.

Seed Production.—Under the usual conditions, the number of seeds produced by an insect-pollinated species depends chiefly upon the success attained in pollination. The abundance of each species, as well as its survival, is determined primarily by the number of seeds that germinate and seedlings that become established. At each step in this

fundamental process of ecesis, animals enter the situation and their coactions largely or wholly determine the number of seeds available, their dissemination, and the final fate of seedling or adult plant. Insect parasites destroy large numbers of seeds and fruits before they mature, and a similar effect is exerted by some birds, such as the nutcrackers and jays. In general, much greater destruction is wrought at the time the seeds are ripening or after seed or fruit has left the parent plant, birds, rodents, and man each having an especially decisive share in this.[556]

It has been found that in some regions practically all the seeds of the limber pine are eaten out of the cones when still green, while in the case of lodgepole pine the toll of cones and seeds taken by birds and rodents is so complete that reproduction rarely occurs until after a fire has driven the animal population out. A single kangaroo rat may store as much as a bushel of grass fruits in its burrow, and harvester ants may gather all the fruits of desert grasses over considerable areas. So great is the consumption of seeds in many species, and trees especially, that adequate reproduction is possible only during years in which climatic and growth conditions cooperate to produce a crop much beyond the needs of the animal members of the community. Such seed production is a consequence of the climatic cycle and marks a maximum phase of the food cycle, which, in its turn, is reflected in a population maximum.

Seed Distribution.—The dissemination of seeds by animals and man may result from each of the four major coactions, namely, food, material, shelter, and contact, but it centers about the first, with the last second, perhaps, in importance. In the case of seeds or fruits utilized as food, successful distribution depends almost wholly upon protection against digestion. The disseminules of most herbs lack such protection more or less completely and are regularly destroyed in the digestive tract of birds but to a somewhat lesser degree in that of mammals. A considerable number of trees and shrubs have been specialized for such distribution by devoting a portion of the fruit to the attraction and reward of the disseminator and by protecting the seed against digestion by means of a stony cover, developed usually by the fruit. Such fleshy fruits are among the most successful migrants, though their distribution is usually local, as fence rows filled with red cedar, sumac, and similar shrubs testify. Nut fruits and cones are collected by rodents in vast numbers, but they are carried little if at all beyond the forest edge, and it is only by chance that a seed here and there escapes consumption.[88,293]

Most effective of all is dissemination by contact and attachment, since the dry fruits chiefly concerned are not used for food by the animals that transport them. The movement of "sticktights" and "tickseeds" is, for the most part, local or at least within woodland, where they abound, but the various burs, such as cockleburs and sandburs, were often carried over considerable distances by migrating buffalo. Carriage

by man has been the outstanding process during the historical period, not merely because of his world-wide migration, but especially also on account of the fact that he produces innumerable disturbed areas in which ecesis is possible. Roadways and trackways have served as universal pathways of migration, in which disturbance is the characteristic feature. In the great majority of species, the carriage has been incidental to the transport of foodstuffs or materials and, hence, wholly unintentional, but in the aggregate it has been far in excess of all other methods of long-distance migration. In addition to actual transport by railroads is the unique action of vortex winds due to passing trains, which have been the main factor in the distribution of ruderal and native species for many hundred miles. No other migration agent is in the least comparable with man in the effectiveness and extent of its action. Water is similar in acting over long distances, but only a relatively small number of seeds and fruits can withstand immersion for more than a few days at most.

COACTIONS OF THE PLANT BODY

Food coactions are concerned where the plant body is employed for food by animals or man. The outstanding coaction of this group is grazing, under which may also be included browsing when trees and shrubs are concerned rather than herbs. The number of instances in which the plant body is utilized for food is incalculable, but these may all be arranged in a few major groups. The latter comprise the coactions between aquatic animals, chiefly invertebrates, and plankton; between insects and leafy shoots; rodents, grazing animals and herbs; browsing animals and foliage; and between a heterogeneous group and wood in various forms. Birds are usually not concerned, since even when they attack seedlings, it is usually for the sake of the seed itself. In this general category belong also the interactions of bacteria, fungi, and other plant parasites with animals, and with other plants as well, but these are not considered in the present account. Man ranges over almost the entire field of coactions, but only the most important ones can be discussed here.

Grazing Coactions.—The primary relation is that of food supply, with the natural assumption that the coaction is wholly beneficial to the animal and injurious to the plant. In the first case, the chief exception is constituted by poisonous plants, such as *Astragalus*, *Delphinium*, *Lupinus*, *Aragallus*, and *Zygadenus*, while minor exceptions are furnished by plants with spines or harmful awns, such as cacti, needle grasses, etc. The damage done the plant by grazing or browsing depends largely upon the life-form. The annual is often destroyed and the perennial herb injured in various ways and to different degrees; low shrubs may be kept in a dwarf, leafless condition, while tall ones and trees are little affected.

On the other hand, grasses, sedges, and similar forms with basal meristem in the leaves and shoot buds near the ground suffer slight damage from the removal of their foliage if this is not too frequent. Every species is injured by overgrazing, but grasses withstand this better than all others and are actually benefited by moderate cropping. This not only removes the dead litter which is undesirable for several reasons but also seems to stimulate the growth of leaves and buds; at least, it has been found that the growth of grasses under complete protection is distinctly less than with properly regulated grazing.

Grassland resists trampling more successfully than any other type of community, though as with grazing the amount of damage is determined by the severity of the process. Trampling, when not too severe, is beneficial in scattering and planting seeds and fruits and, to some degree, offsets the harm done by grazing while fruits are being formed. When animals are crowded as about wells, in corrals, or in bedding grounds, trampling is extreme and usually results in the complete destruction of the vegetation and the initiation of secondary seres.[436] Such areas are marked by colonies of weeds, which serve as indicators of disturbance and persist until the cause is removed. When the disturbance ceases, such seral communities gradually yield to the competition of the returning grasses and the climax grassland is more or less completely restored. A fairly permanent effect of overgrazing and trampling is registered in the short-grass subclimax of the Great Plains, where the taller species are kept down in consequence of their life-forms being more susceptible to injury. The composition of grassland may also be much modified because earlier or more palatable species bear the brunt of the grazing coaction, even to the point of disappearance.[103] The most striking change of this type, however, is to be encountered in grass associations containing scattered shrubs, such as sagebrush or mesquite. The latter are eaten much less than the grasses and, as a result, increase correspondingly in number, until they appear to dominate the entire community. Experimental exclosures have demonstrated that the shrubs gradually disappear under the competition of the grasses when the latter are protected from grazing and indicate that much of the large area covered by sagebrush, mesquite, and other shrubs is actually climax grassland.[91]

Rodent Coactions.—In all essential respects, these are similar to the relations that exist in the case of grazing or browsing by the larger mammals.[523] The main differences lie in the fact that the effect exerted by each individual is much smaller and more localized, and that control, either for practical or research purposes, is much more difficult. Apart from the influence upon the seed crop already mentioned, the major damage done by rodents is inflicted upon the leafy shoot, though pocket gophers, moles, and other tunneling forms do great injury to roots and

underground stems, both directly and indirectly.[448] The coactions differ from genus to genus and family to family and depend almost wholly upon habits and life history. The wandering jack rabbit behaves much as do cattle but on a smaller scale (Fig. 27); the social prairie dog works great changes in the plant covering of his towns, and the provident cony cuts and stacks hay for his long winter above timber line. Although more intelligent as to poisonous plants and apparently less susceptible, also, rodents do fall victims to the most poisonous species. Spines and thorns likewise exercise an influence, though some species, such as the woodrat or packrat, actually turn these to good purpose in the construction of nests.

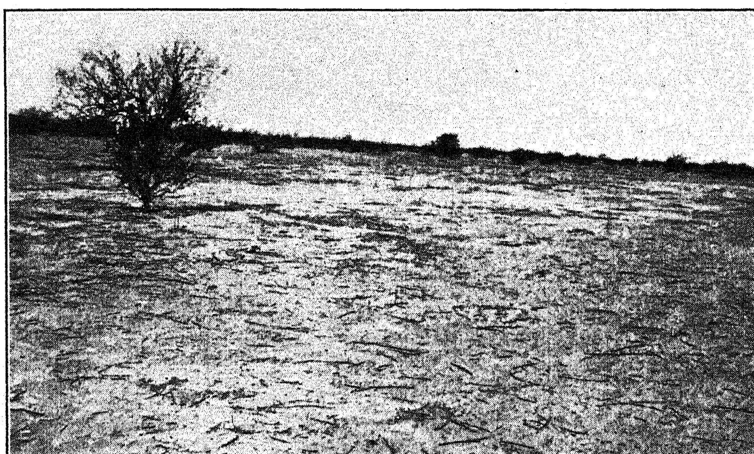

FIG. 225.—General denudation by kangaroo rats in desert scrub in Arizona.

Although the effect produced by a single rodent is small, the total influence of a vast population of many species is great and often decisive. When they are more or less restricted in their movements, as in the case of prairie dogs or kangaroo rats, the final affect may be as striking as in an extreme case of overgrazing and trampling by cattle (Fig. 225). The original grasses of a prairie-dog town are often completely replaced by annual weeds, the area about a kangaroo-rat mound may be wholly bare, and the runways of jack rabbits may be almost as well-worn as cow paths.[547] Rodents exert little or no effect in planting seeds, largely because of the heavy toll they take in most cases, though burrowing forms and pack rats have more value in this connection.

Coactions upon woody plants are less frequent, but they are not without importance. Perhaps the most outstanding examples are furnished by the beaver, which employes aspen and birch in particular for construction materials as well as food.[15] Because of their choice of trees, much more damage is done by porcupines, rabbits, and other bark-eating

rodents, which may kill a large tree in consequence of consuming only a portion of the bark.[300] Similar consequences of a relatively small coaction are to be found in the damage to trees wrought by sapsuckers among birds.[336,336a]

Human Coactions.—It is evident that man stands alone with respect to the number and variety of his coactions with plants. Like the animals, he derives, directly or indirectly, his entire food supply from plants and he has produced far-reaching changes by learning to control this supply. He is likewise susceptible to many coactions from the plant and one of his chief tasks has been to understand and control these, not merely in the case of foods, poisons, and drugs, but especially also in that of parasitic bacteria. The most striking coactions have had to do with mass effects upon vegetation, as represented by fire, cutting, and clearing. All of these processes bring about the destruction of one community in whole or in part and its replacement by another, either as a result of planting or in consequence of succession. These have been discussed briefly in preceding chapters and it merely needs to be further emphasized that all man's uses of plants, both native and cultivated, rest upon the basis of coactions. While they differ in details, cultivated fields and natural communities bear the same general relation to physical factors, exhibit the same basic processes of competition and reaction, and are subject to similar coactions on the part of man and animals.[520]

Sequence of Coactions.—In many cases, the influence of plants and animals upon each other does not stop with the immediate or primary coaction. The development of a new relation or the concrete working out of an old one sets in motion a train of mediate or secondary consequences in which an entire series of species or communities may be involved.[389,391] The introduction by man of a new fruit or crop for food or materials often means the bringing in of fungi or insects parasitic upon it and ultimately of the parasites upon these. With the seed of grains come those of weeds; the latter not only demand the further attention of man, but they also produce new interactions with native species and their plant and animal associates, the waves of influence extending far beyond our present knowledge. One of the final effects is to be found in the establishment of quarantine regulations, both national and state, to prevent or control such coactions.

The best known of coaction sequences have followed upon the introduction by man of the English sparrow and starling into the United States, of the thistle into Australia, and of the bumblebee into New Zealand, but the same process has been exemplified in the case of every cultivated species brought from abroad and every stowaway, whether weed, fungus, or insect. The clearing or breaking of ground for cultivation, the cutting of trees for timber, and the burning of forests have all

set up sequences of far-reaching significance, the understanding of which is indispensable to scientific agriculture and forestry and to conservation especially. One of the most illuminating examples of these complex sequences is found in the effect of man upon predatory animals. The complete destruction of the latter appears to be a simple and beneficial primary coaction, until it is found to be accompanied by an increase in the rodent population with a corresponding decrease in the yield of grazing range or cultivated field. In short, it tends to defeat in some measure the very purpose it was designed to promote—the greater production of cattle and sheep. The protection of game animals—in itself an exceedingly desirable objective—similarly leads to far-reaching sequences of coactions, as in the case of deer, elk, and bison in national parks or forests.[1]

CHAPTER XVII

PLANTS AND PLANT COMMUNITIES AS INDICATORS

Every plant is a product of the conditions under which it grows and is, therefore, a measure of environment. It indicates in general, and often in a specific manner, what other species would do if grown in the same place. The dominant species are the most important indicators, since they receive the full impact of the habitat usually year after year. Furthermore, plant communities are more reliable indicators than individual plants. It has been seen that in the development of vegeta-

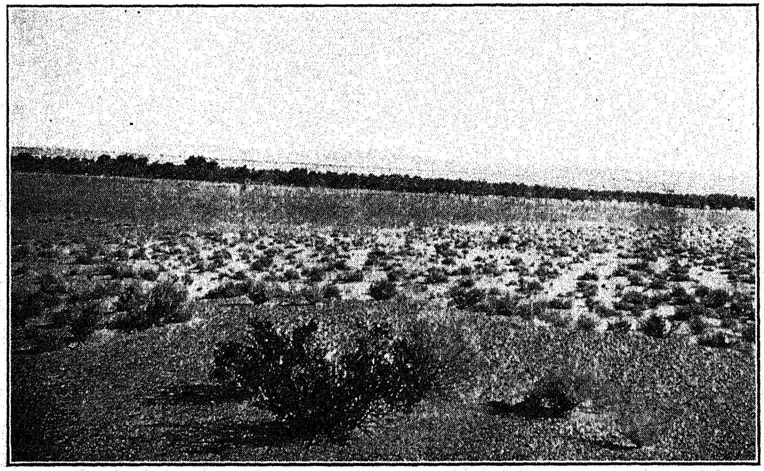

FIG. 226.—Mohave River valley, showing zones of vegetation due to different depths of ground water. Desert scrub in the foreground, salt grass in the lowland back of the desert scrub, and flood-plain forest of poplar, willow, and mesquite along the river. (*U. S. Geol. Survey, Photo by D. G. Thompson.*)

tion species are not indiscriminately mixed without regard to their fitness to be companions but that the members of the community are adapted to each other and to their common surroundings. A community of hard maple, buffalo grass, spike rush, creosote bush, and sea blite would be an absurdity. Each species thrives in a habitat quite different from that of the others. One immediately associates beech, linden, spicebush, and various other trees, shrubs, and herbs of similar habitat requirements with hard maple. In the same way, desert species such as cacti, yucca, etc., are associated with the creosote bush. Each plant and community, moreover, brings to mind a more or less definite soil or climate.

A plant or community may indicate a deficiency or an excess of water and often accompanying secondary or concomitant factors. Cacti, yucca, sagebrush, and xerophytes in general are associated with habitats of low water content as well as usually with high temperatures and low humidity. Cattails and bulrushes, as well as other hydrophytes, indicate in a general way an excessive water supply and consequent poor aeration. Greasewood, saltwort, and other halophytes denote an excess of soil solutes just as definitely as such woodland forms as wild ginger and

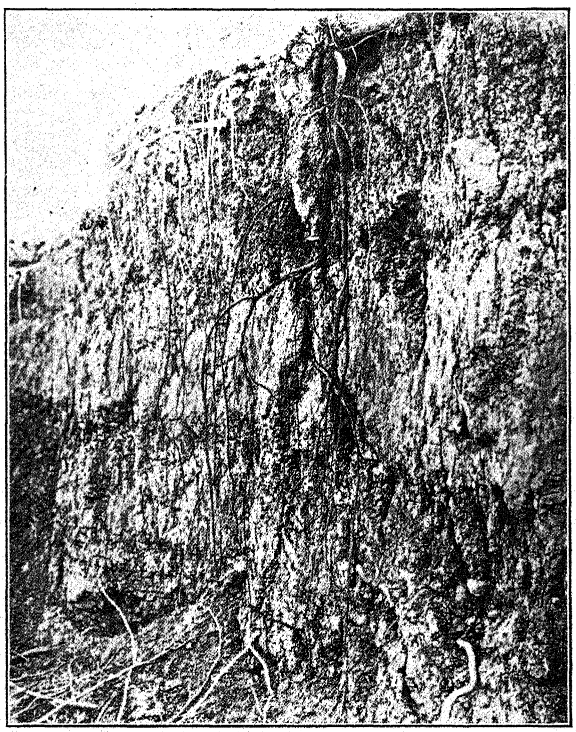

Fig. 227.—Cut bank of Santa Cruz River near Tucson Ariz., showing the deep roots of the mesquite (*Prosopis*). (*Photo by V. M. Spalding, Carnegie Inst. Wash., Pub.*, 113.)

ginseng indicate, with other woodland species, habitats with low light intensities. A seral community, *e.g.* reed swamp, not only indicates the present condition of the habitat but also what the previous conditions were and what future conditions will be.

Plants are indicators of *conditions, processes,* and *uses* (Fig. 226). Many species such as salt grass (*Distichlis*) and reed (*Phragmites*) indicate a water table at or near the surface soil; others such as Washington palm (*Washingtonia*) and greasewood (*Sarcobatus*) indicate ground water at a greater depth, while the mesquite (*Prosopis*) is an indicator of a deep water table, the roots sometimes extending to a depth of 30 to

50 feet (Fig. 227). In fact, certain species are confined almost completely to areas with specific water-table depths.[347] Various species indicate such processes as erosion, lumbering, trampling, fire, etc. Others are of great value in indicating the uses for which lands may best be employed, *viz.* agriculture, grazing, forestation, etc.[91]

INDICATORS OF AGRICULTURE

The most reliable natural indicators of the agricultural possibilities of a region are to be found in its native vegetation.[461] For many centuries, the natural vegetation has been sorted out by climate as well as by the soil in its process of development, until usually only species well adapted to a given environment now occur in abundance. The growth of the plant cover is a measure of the effects of all the conditions favorable or unfavorable to plant development. The natural plant cover, if properly interpreted, indicates the crop-producing capabilities of land better than any series of meteorological observations or soil analyses (Figs. 228 and 229). This does not minimize the importance of the study of environmental factors, since the significance of the various types of vegetation can be interpreted only by an understanding of the conditions under which the plants grow, especially where agriculture is not already well established.

Forests as Indicators.—Since the earliest settlements in America, agriculturists have been accustomed to judge the quality of land by the forest trees growing upon it. The pioneers in the Ohio Valley who settled on lands covered with sugar maple and beech were more prosperous than those on oak and pine lands. Forests should be examined not only as to the species but also as to the form and size assumed by the trees growing in arable soils. For example, post oak (*Quercus stellata*) and blackjack oak, (*Q. marilandica*) are very different in their habit of growth on upland and lowland or on sterile sandy soil. When thus considered, forests form a safe criterion for evaluating the potential productivity of the land. This is especially true where tree growth is correlated with the development of the shrubs and perennial herbs of the forest floor. Not only the market value of the land but also the tax rate has been frequently determined by the type of vegetation. The accuracy with which experienced farmers were able to evaluate the productivity of timberlands by their forest growth excited the wonder even of agricultural investigators. Thus, "black oak and hickory uplands," "gum bottoms," "hackberry hummocks," "post-oak prairie," "red-cedar prairie," etc., each had certain cultural values or peculiarities of soil well understood by the farmer.[235]

Many years ago, it was noted that

> . . . in the long-leaf pine uplands of the cotton states, the scattered settlements have fully demonstrated that after 2 or 3 years' cropping with corn,

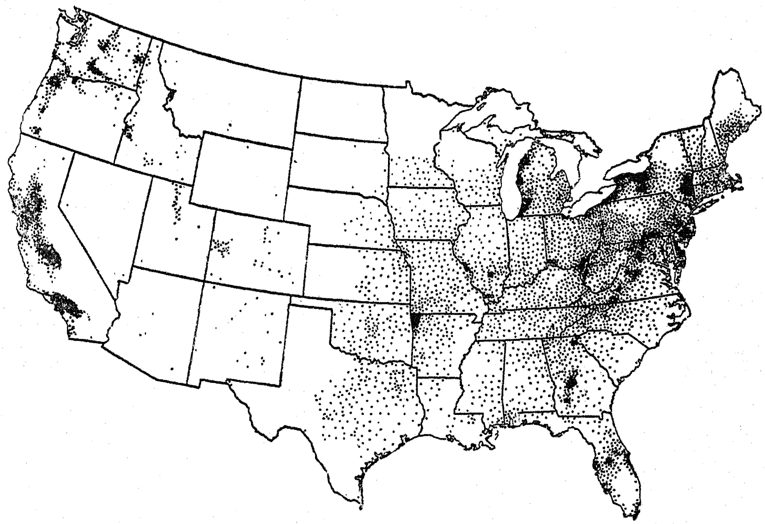

FIG. 228.—Distribution of fruit and nut trees in 1919. Each dot represents 1,000 acres. The greatest areas of production of tree fruits such as apples, peaches, pears, chestnuts, pecans, etc., and such bush fruits as blackberries, currants, and raspberries (aside from irrigated districts) are in those portions of the United States formerly occupied by forest trees and shrubs. (*U. S. Dept. Agr.*)

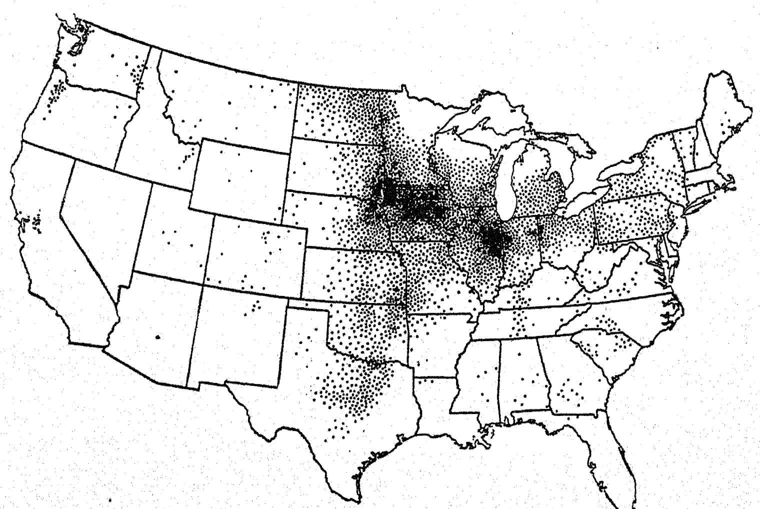

FIG. 229.—Distribution of oats in 1919. Each dot represents 10,000 acres. The cereal crops, *viz.* corn, spring and winter wheat, oats, barley, sorghum, and millet, all of which are grasses, have their center of greatest production in that portion of the United States originally covered by grassland. (*U. S. Dept. Agr.*)

ranging as much as 25 bushels per acre the first year to 10 and less the third, fertilization is absolutely necessary to further paying cultivation. Should the short-leaved pine mingle with the long-leaved, production may hold out for 5 to 7 years. If oaks and hickories are superadded, as many as 12 years of good production without fertilization may be looked for by the farmer; and should the long-leaved pine disappear altogether, the mingled growth of oaks and short-leaved pine will encourage him to hope for from 12 to 15 years of fair production without fertilization.[236]

Grasslands as Indicators.—The relation between the native vegetation and possibilities of the land for crop production is well illustrated by the various types of grassland in central North America. The great grassland area extending across the Mississippi Valley from the forests of the East to the foothills of the Rockies is not characterized by a uniform vegetation throughout. The tall-grass prairies of the eastern portion are distinctly different from the short-grass plains of the West and Southwest, and between these two regions is a broad belt of mixed grassland where tall and short grasses intermingle. The chief causes of these differences in grassland vegetation are the differences in the quantities of soil moisture supplied by the rainfall and the length of time during which soil moisture is available. Decreased relative humidity westward is also an important factor. Differences in soil structure, resulting from differences in climate and vegetation during its development, are also pronounced. These factors, which have so largely determined the type of grassland, exert striking influences on the development of both root and shoot and, hence, influence crop growth and yield.

Tall-grass Prairies.—The tall-grass prairies constitute the grasslands of Minnesota, Iowa, Illinois, Indiana, and Missouri, as well as approximately the eastern one-third of the Dakotas, Nebraska, and Kansas, and large areas in Oklahoma (Fig. 230). The grasses are from 1.5 to over 5 feet tall and are rooted to an equal or greater depth in the dark-colored, rich, moist soils. They form a rank growth, mostly of the sod type, due to extensive rhizome development, and usually continue growth throughout the entire summer. This is possible because of the presence of abundant soil moisture. Even in the drier portions the soil is usually moist to a depth of several feet and moisture is continuous to the water table in the wetter areas. The surface soil may dry out each year and drought may occur in late summer and fall, but the subsoil, into which the deeper roots of the vegetation penetrate, is permanently moist. Such conditions should promote the development of numerous, deeply rooted species and, in fact, prairie vegetation is characterized by this type of root habit.

Among the very numerous species of grasses that occur, the most important ones are the bluestems (*Andropogon*), tall panic grass (*Panicum virgatum*), tall marsh grass (*Spartina michauxiana*), wild rye (*Elymus*

canadensis), needle grasses (*Stipa*), June grass (*Kœleria*), and dropseed (*Sporobolus*). In addition, there are very numerous and extensive societies of legumes, composites, mints, roses, etc.

Conditions Indicated for Crop Growth.—The presence of a continuous cover of tall, deeply rooted grasses indicates conditions favorable for the production of cultivated plants of similar habit, a fact fully substantiated by the excellent yields of wheat, oats, and corn. The continued growth of these grasses throughout the season, with the late period of flowering and seed production among most of them, indicates a long, favorable growing season uninterrupted by a deficiency of soil moisture. The abundance of water in soil and subsoil is further attested by the

FIG. 230.—Upland tall-grass prairie in eastern Nebraska. Needle grass (*Stipa spartea*) is the most conspicuous species.

presence of a great many other herbs, many of which extend much deeper than the grasses and absorb the water that percolates downward through the surface soil. There is water enough for both grasses and legumes, as well as composites, etc.[567]

The deeply rooted species have favorably modified the subsoil to great depths, enriching it with nitrogen, adding humus by root decay, as well as making it more porous. As a result of absorption, vast stores of nutrients have been brought from the deeper soils and, upon the death of the tops, deposited in the surface soil. Thus, the tall-grass prairie furnishes the most productive region for agriculture.[17]

Short-grass Plains.—The short-grass plains extend over areas in western Nebraska and include much of the western half of Kansas, eastern Colorado, western Oklahoma, northwestern Texas, and northern

New Mexico. They also occupy extensive areas in eastern Wyoming and Montana. Outlying detached areas occur west of the Rocky Mountains. While the tall-grass prairies may be likened to a luxuriant meadow, the short-grass plains resemble a closely grazed pasture (Fig. 231). The grasses are truly short; the leafy stems are usually only 3 to 8 inches tall, although the flower stalks may be 12 to 18 inches high. Absorption regularly takes place in the 16 to 24 inches of surface soil, below which dry subsoil occurs.

FIG. 231.—Short-grass plains in eastern Colorado. The dominant grasses are blue grama (*Bouteloua gracilis*) and buffalo grass (*Bulbilis dactyloides*).

The grasses form a low mat or sod due to extensive propagation by rhizomes and stolons. In the drier portions, much soil surface is exposed, but under more favorable moisture conditions, the sod mats are more nearly continuous. Because of deficiency of soil moisture and severe summer drought, the vegetation matures early, seeds ripening within 30 to 60 days after the inception of growth. The grasses "cure" on the ground but may resume growth upon the advent of opportune showers. Precipitation is so limited that the soil is seldom moist below a depth of 2 feet. Water penetrates slowly, owing in part to the high water-retaining power of the surface layers of fine sandy-loam or clay-loam soils and also to the vigorous absorption by the short grasses. The small amount of moisture, if any, stored during the winter season in the foot or two of surface soil, together with the rainfall of spring and early summer, may enable growth to continue until early July, when usually all the soil moisture is exhausted. As a consequence, deeply rooted tall

grasses and other herbs are frequently excluded, and the typical short-grass cover is very uniform and monotonous as a result.*

During unusually dry years even short grasses may fail to flower, but during wet ones growth may continue without interruption. The continued penetration of water to only 16 to 24 inches has resulted in a concentration of the leached salts and alluviated clay, which form a carbonate layer varying from 8 to 24 inches in thickness and sometimes occurring at depths of only 8 to 10 inches. Below the hardpan occurs a dry subsoil. By hindering water penetration in consequence of vigorous absorption, the native vegetation has exerted a profound effect upon soil structure and soil profile in the short-grass plains.

When the natural vegetation is destroyed by cultivation, the depth of penetration is increased even if the land is continuously cropped, and with alternate years of cropping and summer fallowing this depth is even greater. In the former case, water seldom penetrates below 2 to 3 feet, and under the latter practice only rarely to 5 or 6.[464] Thus, owing to low precipitation, usually less than 20 inches, high run-off, and great evaporation, the deeper subsoil is constantly dry. Under conditions of cropping, root activity is confined, as among native species, to the surface layers in which the available moisture supply is exhausted almost annually.

The chief grasses of the plains are few in number and quite similar in habit. Conspicuous among them are the blue and hairy grama grasses (*Bouteloua gracilis* and *B. hirsuta*), buffalo grass (*Bulbilis dactyloides*), Muhlenberg's ring grass (*Muhlenbergia gracillima*), and wire grasses (*Aristida*). Since these grasses, with others of similar habits, annually absorb nearly all of the available water, relatively few other herbs are present. Numerous shallow-rooted annuals, various cacti, and certain legumes, etc., however, occur more or less sparingly.

Conditions Indicated for Crop Growth.—The indicator significance of the vegetation of the short-grass plains is very distinct from that of the tall-grass prairies. It is a region of dry farming, grazing, and crop production under irrigation. Short grasses characterize areas where, each year, all available moisture is used by the plants, the supply often being exhausted early in the summer. The presence of a carbonate layer at a depth of 1.5 to 2 feet indicates the usual depth to which water penetrates and delimits the depth to which absorption of water and nutrients regularly occurs. The low stature of the plants is correlated with drought. Tall grasses with leaves exposed on elongated stems are not so well fitted to withstand desiccation, nor are their roots so well adapted to absorb moisture from the surface soil. Roots fitted for surface absorption are an essential adaptation of grasses of the plains.

* For the relation of the short-grass community to the mixed prairie, see p. 465.

Cultivated plants, too, when grown here, must adapt themselves to these conditions, although the removal of the sod and the maintenance of a granular mulch permits somewhat greater water penetration. Their response is similar to that of the native plants, *i.e.* low stature and shallow but widely spreading root systems. These are much more profusely branched than normally, many roots occurring just beneath the surface of the soil. Early maturing crops like winter wheat, although of uncertain but sometimes heavy yield, do best. Like the rapidly maturing plains grasses, they may ripen seed before the soil moisture is exhausted. Many small grains and short-season corn are widely grown and the sorghums are well represented in the southern part of the area.

The high productivity of soil and subsoil is clearly shown where irrigation water is applied. In the moistened soil, abundant crops of alfalfa, sugar beets, and other deeply rooted plants produce excellent yields, under the otherwise favorable climate.[261] Owing to the uncertain distribution of precipitation, however, crop production without irrigation is always hazardous. Much of the area should always remain unbroken range land.

Mixed Prairie.—The mixed-prairie association covers a wide area between the tall-grass prairies on the east and the short-grass plains on the west. It occupies considerable portions of eastern and central Montana, central and western North and South Dakota, eastern Wyoming, and the central parts of Nebraska and Kansas. It extends farthest west on sandy soils which permit the water to penetrate readily, frequently covering isolated sandy areas surrounded by short grasses. Pure short-grass cover extends farthest east on heavy clay soils into which water penetrates slowly, a condition unfavorable for deeply rooted tall grasses. Mixed prairie is limited on the east by increased soil moisture sufficient to support a continuous growth of tall-grass vegetation which shades out the understory of short grasses.

The most significant distinction between mixed prairie and tall-grass prairie is the almost universal presence of one or more short grasses or sedges as a lower layer under the taller species. The tall grasses are thus intimately mixed with the shorter ones. In lowlands of greater water content, the tall grasses dominate; on dry hilltops, they may almost completely give way to short grasses. But over the area as a whole, the medium water relations limit the growth of the tall grasses, which frequently resort to the bunch habit, short grasses occupying the interspaces (Fig. 232).

On the western and southern borders of this association, water content is usually entirely exhausted by midsummer and the subsoil is always dry. Here, the carbonate layer varies from 20 to 30 inches in depth. During July, the plants pass into a drought-rest condition from which they may be revived by occasional showers. But where the deeper-

rooted, later-blooming bluestems form the upper story, this occurs less frequently, and through periods of wetter years the subsoil may be permanently moist. No moisture, however, is lost to the vegetation by percolating beyond the root depth. This is shown by the presence, even on well-drained silty or clayey soils, of a layer of carbonate accumulations at a depth of 5 to 6 feet, rainfall not affording enough moisture to percolate through and carry it away. With increasing water penetration, the carbonate layer becomes deeper and in the tall-grass prairies entirely disappears.

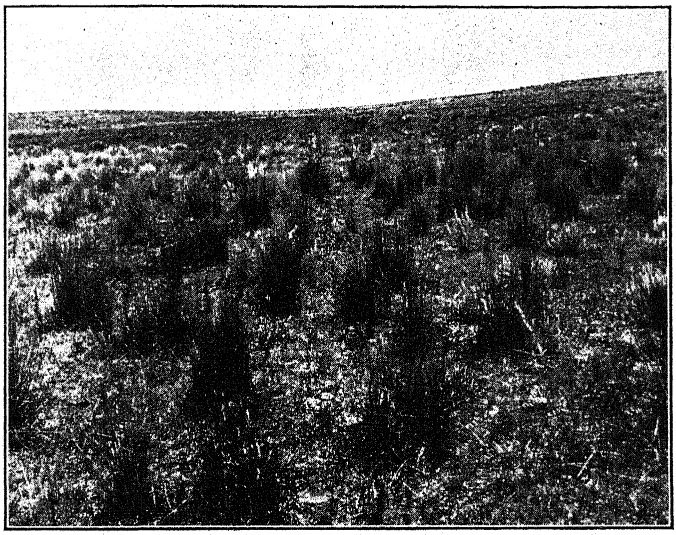

FIG. 232.—Mixed prairie; the bunches are little bluestem (*Andropogon scoparius*), the lower layer consists of various short grasses and sedges.

Many species of both adjacent grassland communities are represented. Among the most important tall grasses are wheat grasses, needle grasses, June grass, little bluestem, and wire grasses. The short-grass layer is made up largely of buffalo grass, blue and hairy grama, and certain grass-like sedges.

Conditions Indicated for Crop Growth.—The presence of short grasses, with their root systems excellently distributed for surface absorption, together with the marked development of the shallower portion of the root system of many of the taller ones, points at once to their dependence upon moisture afforded the surface soils by light showers. The great masses of finely branched roots of both tall and short grasses occurring in the deeper soils indicate available water content at these levels, also. But the absence of a continuous cover of tall grasses often shows a periodic deficiency in the water supply. The less abundant the late maturing tall grasses (under conditions undisturbed by grazing or other-

wise) and the more abundant those of a shorter growing season the greate is the probability of water exhaustion in midsummer and crop failure. r

It is in the mixed prairie that the highly productive farm lands of the tall-grass prairies give way to the less productive ranch lands of the short-grass plains. Corn growing becomes less important, listing becomes a common farm practice, and the relative acreage of wheat is greatly increased. Timothy and clover give way to wild grasses and alfalfa; the carrying capacity of pastures gradually decreases.[17] The water content is the controlling factor. Here, crops root at intermediate depths, varying locally with seasonal distribution of rainfall but relying less largely upon absorption from the surface foot than in the short-grass plains and more upon moisture in the deeper soil.

INDICATORS OF SOIL TYPE

Extensive studies in the Great Plains have shown that under the same precipitation and other climatic conditions the native vegetation may vary greatly and, in fact, different communities may occur within a radius of only a few miles.[461] These differences are due to the type of

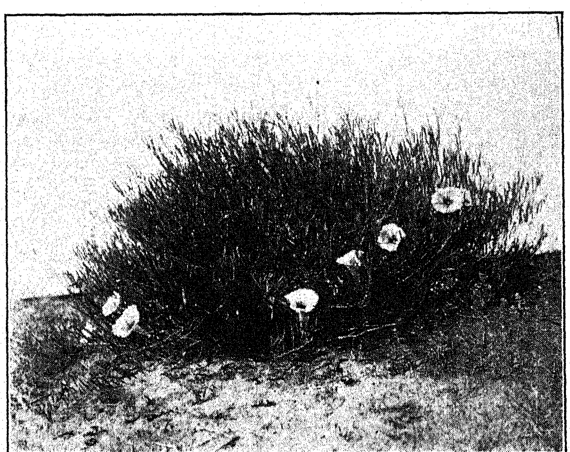

Fig. 233.—Bush morning-glory (*Ipomœa leptophylla*), an indicator of sandy soil. The plant is perennial from an enormous root which serves for storage of water and food.

soil. On the hard, compact, very fine sandy- and silt-loam soils, which are by far the most extensive, the buffalo and grama grass community develops as already described. Where the soil contains an admixture of sand, run-off is greatly reduced and the water penetrates to greater depths, often to 3 or 4 feet. This sandy-loam type of soil is clearly indicated by the abundance of certain characteristic species which are taller and more deeply rooted than are the short grasses on the "hard lands." Chief among these are wire grass and *Psoralea* which form an open growth in the grama-grass sod (buffalo grass being rarely found)

since moisture in the deeper soil is not sufficient to produce a continuous growth of the taller, deeply rooted plants.

Where the soil becomes so sandy that all of the rainfall is absorbed and there is no run-off, the bunch-grass (*Andropogon scoparius*) type of vegetation prevails. This tall, deeply rooted grass is accompanied by the sandhills' bluestem (*Andropogon hallii*), sand reed (*Calamovilfa*), sand sage (*Artemisia filifolia*), bush morning-glory (*Ipomœa leptophylla*), etc., which constitute, with the grama grasses, a mixed prairie (Figs. 233 and 234).

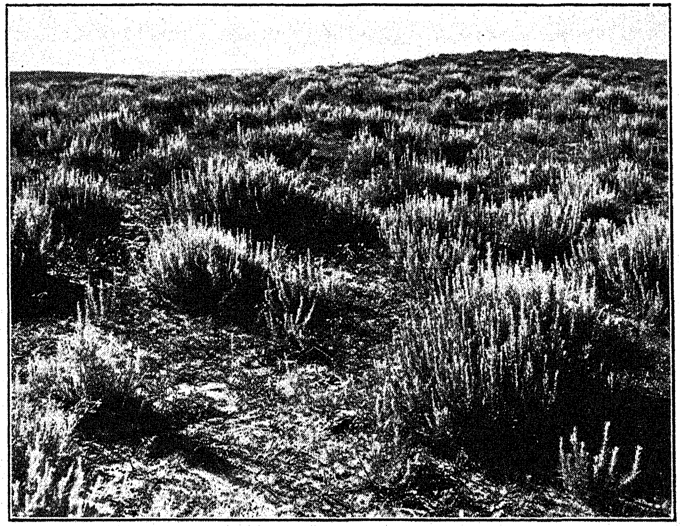

FIG. 234.—Sandhill sage (*Artemisia filifolia*), an indicator of sandy soil.

Short-grass land indicates high run-off and limited water penetration and a growing season shortened by a limited water supply. Such land is not at all adapted to late-developing, deeply rooted crops such as corn, although early-maturing crops, such as winter wheat, sometimes give a good yield. Owing to the high fertility, crops make a rank growth when water is plentiful early in the season and are thus poorly fitted to withstand drought.

Wire grass indicates soil into which almost all of the rainfall penetrates and where surface evaporation is greatly reduced. The moisture is distributed to a considerable depth and when drought threatens, plants are able to draw on the reserves found in the deeper layers of soil. The native vegetation indicates this longer growing season. Fertility is still sufficiently high so that crops grown on wire-grass land, even during favorable years, are almost as good as on short-grass land, and during dry years much better crops are produced.

Bunch grass indicates soil of a texture that insures the penetration of practically all of the water that falls. Little water is lost directly by

evaporation from the sandy soil. Crop growth is much less luxuriant on this land owing to decreased fertility; the retardation in growth itself aids in conserving the water supply. The native plants indicate a long season for growth, and, like them, the roots of crops spread widely and deeply and plants rarely wilt because of drought. Lands of the bunch-grass and wire-grass type are locally known as "corn land."

Crop failures occur most often on short-grass land and least often on bunch-grass land. During favorable years yields are highest on the former and least on the latter. Wire-grass land represents a safe inter-

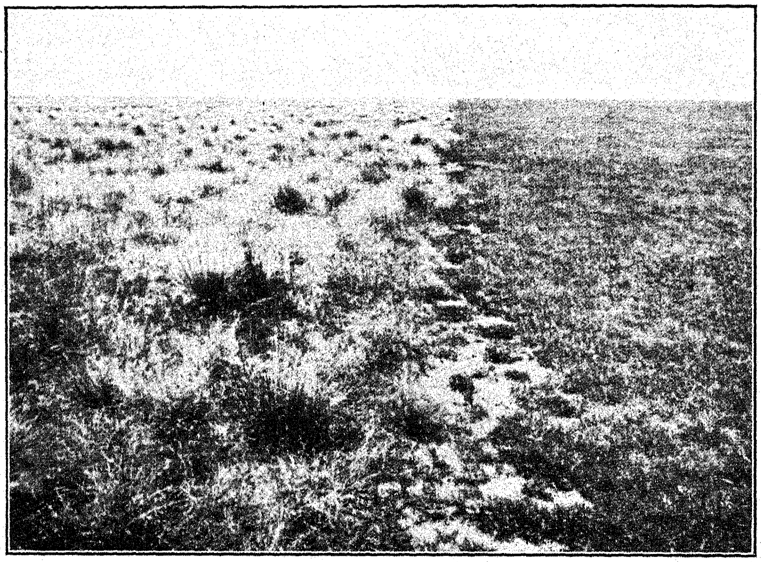

FIG. 235.—Wire-grass community established as a result of breaking short-grass land, Yuma, Colorado. (*After Shantz.*)

mediate condition; during favorable years crops are almost as good as on short-grass land, and during dry years a fair crop can often be produced. Many of the older settlers in eastern Colorado have moved from short-grass land on to wire-grass land, or even on to bunch-grass land, where there is much less likelihood of crop failure. The newcomer in the region, however, almost invariably chooses the hard or short-grass land because it is darker in color and looks like the soil he has been accustomed to farm successfully in the East.[461]

Why a Knowledge of Plant Succession is Necessary.—From the preceding it may be seen that in eastern Colorado short-grass vegetation indicates a loam soil, wire grass a sandy loam, and bunch grass a sandy soil. These correlations do not hold eastward under a higher rainfall, where the subsoil of even compact loam may become quite moist and favorable for the growth of bunch grass. Careful studies must be made

of various plant communities in relation to their physical environment before their indicator significance becomes clear. A knowledge of successional sequence is also imperative. When short-grass vegetation is plowed under and the area subsequently abandoned for a time, run-off is decreased, water penetration encouraged, and loss by absorption greatly reduced. Upon such areas of loam soil, there often develops a thriving community of wire grass, the wind having brought in the propagules from plants perhaps many miles away (Fig. 235). This community persists for a long time but after a period of 20 to 30 years the area returns to the short-grass climax. Similarly, when wire-grass land is broken, bunch-grass vegetation may temporarily gain possession of the area. If wire grass is repeatedly burned there is a tendency toward the development of a pure short-grass cover.[461]

INDICATORS OF ALKALI

In large portions of the western half of the United States, rainfall is so light that the excess salts of the soil have not been leached away and carried to the ocean but have accumulated, especially in lowlands, forming alkali spots often of great extent. Such areas are characterized by plant communities especially adapted to secure water from strong soil solutions. Some species are able to tolerate more alkali than others; some will not endure it but make a fair growth in dry, non-alkaline soil. Could the prospective settler foretell what types of vegetation indicate the presence or absence of alkali salts in quantities likely to be injurious to cultivated crops and what types indicate conditions favorable or unfavorable for dry farming, it would be distinctly advantageous.

Accordingly, several investigators in the United States Department of Agriculture set to work to determine the indicator significance of the various plant communities.[275] An extensive area near Great Salt Lake in Utah was selected for this study, since it was representative of Great Basin conditions. Some of the soils contained an excess of alkali; much of the land was still covered by the original plant communities; but enough had been tilled either by methods of dry-land or irrigation farming to serve as a check. Alkali areas are characterized by relatively few species which form a very open cover of vegetation. Boundaries between the different communities are, moreover, often very abrupt and distinct.

Sagebrush, which is the most important type of vegetation in the Great Basin, makes an excellent growth on the non-alkaline, light-textured, deep, well-drained soils of the uplands (Fig. 236). White sage, a low-growing grayish half-shrub, occupies the finer-grained, easily puddled soils, where the subsoil is saline. The large, woody, somewhat spiny and bushy-topped shadscale occurs on more gravelly soil with a saline subsoil (Fig. 237). In certain areas it is accompanied by grease-

wood, a spiny, woody shrub 2 to 5 feet tall and tolerant of considerable salt. On lower ground, extensive salt-grass flats give way to even more alkaline areas characterized by saltwort and species of similar alkali tolerance.

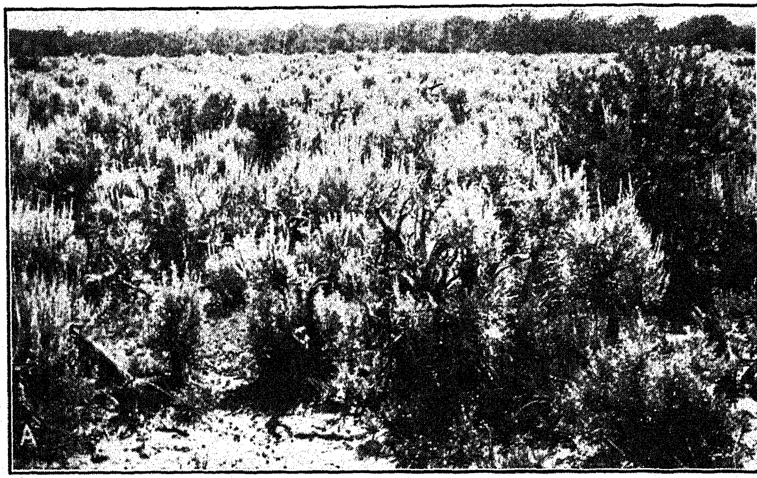

FIG. 236.—A close stand of sagebrush (*Artemisia tridentata*) indicating a deep, porous soil.

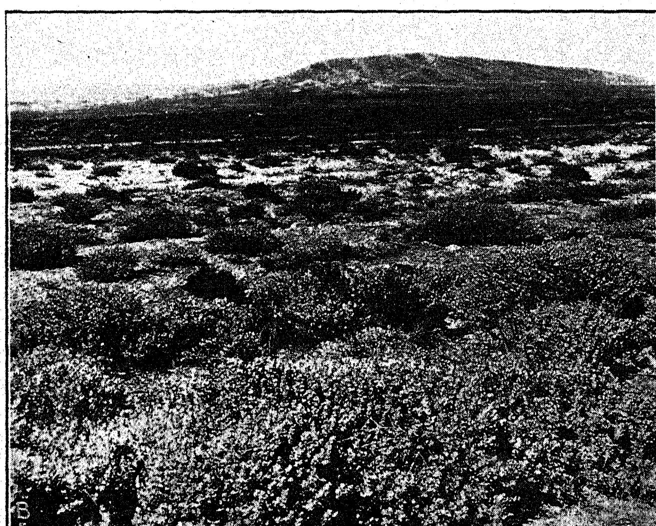

FIG. 237.—Shadscale (*Atriplex confertifolia*), indicating saline soil.

After a thorough study of the water content of the soils in each community together with analyses of their salt content (90 per cent of which is NaCl), and an investigation of root distribution, the following indicator significance was determined for each (Table 10):

TABLE 10.—SOIL CONDITIONS AND INDICATOR SIGNIFICANCE OF PLANT COMMUNITIES

Community	Soil, water content, roots, etc.	Salt content		Capable of crop production	
		First foot	Deeper	Without irrigation	With irrigation
Sagebrush (*Artemisia tridentata*)	Light-textured soil, low run-off. Plants very deeply rooted	Non-saline, usually dry in summer	Non-saline, usually dry in late summer	Yes	Yes
White sage (*Kochia vestita*)	Finer soil, easily puddled, limits penetration of water. Plants rooted in surface 1.5 to 2 feet	Non-saline, usually dry in summer	Saline, usually dry in late summer	Precariously in wet years	Yes, if alkali can be removed
Shadscale (*Atriplex confertifolia*)	More gravelly soil, roots 2 to 3 feet deep	Non-saline, usually dry in summer	Saline, usually dry in late summer	Precariously, more favorable than *Kochia* land	Yes, after alkali is removed
Greasewood-shadscale (*Sarcobatus vermiculatus* and *Atriplex confertifolia*)	Fair water content in surface foot, well drained in summer. Moist below 2 feet. Roots of greasewood 6 to 7 feet deep	Saline or non-saline, usually dry in summer	Saline, moist	No	Yes, after alkali is removed
Grass flats (*Distichlis spicata*, *Sporobolus airoides*)	High water content, good even in summer. Roots shallow	Moderately saline, moist	Moderately saline, moist	Probably not	Possibly with drainage
Salt flats (*Salicornia utahensis*, *S. rubra*, *Allenrolfea occidentalis*)	Moist to very wet. Plants mostly shallow rooted	Much salt, moist to wet	Saline, moist to wet	No	No

FIG. 238.—Aspen forest with *Erigeron*, *Geranium*, etc., indicating the weed type of grazing.

The salt content in the soils of the several communities decreased from 2.5 per cent in the salt flats to 0.8 per cent in the greasewood, while the sagebrush soil had only 0.04 per cent. Thus, it may be seen that each plant community indicates not only a certain concentration of alkali or freedom from alkalinity but also other edaphic conditions upon which the success or failure of crop production directly depends. For example, a good stand and growth of sagebrush indicates land that is well adapted to both dry and irrigation farming; but where the stand is thin and the growth poor, the depth of good soil is usually too limited for profitable crop production, at least without irrigation. Conversely, greasewood indicates land unsuitable for dry farming, but it may be made to produce good crops when the excess salt is removed by irrigation and drainage. These general principles probably apply, in the main, throughout much of the Great Basin.

INDICATORS OF GRAZING

In grazing practice, four classes of stock must be considered, namely, cattle, horses, sheep, and goats.[91] Each has more or less definite preferences as to the type of vegetation grazed and each affects the pasture or range in a markedly different manner. Cattle and horses prefer grass, sheep prefer other herbs and weeds, and goats prefer shrubs or "browse" (Fig. 238). Thus, a uniform community of grass indicates grazing for cattle and horses; one of non-grassy herbs, grazing for sheep; while browse indicates pasture land for goats. Ecotones between chaparral and grassland or desert scrub and grassland indicate mixed grazing where various types of stock may profitably be handled together. In fact, this is often true of various grassland areas most of which have an abundance of non-grassy herbs. Montane forests, especially those of the open, grassy, yellow-pine consociation, and various woodland communities are also indicators of grazing. So, too, are the meadows, parks, and areas of aspen in subalpine forests. Many potential grazing lands give a greater economic return when used for crop production. Such are the tall-grass prairies, much of the mixed prairie, and even short-grass plains, and only the poorer areas with a scantier growth of vegetation are left for grazing.

INDICATORS OF OVERGRAZING

The highest grazing efficiency consists in producing the largest amount of forage from a pasture or range each year. Experiments have shown that the removal of the herbage several times each growing season, especially if the first harvest is made a short time after the beginning of growth in spring, seriously weakens the plants and immediately decreases their forage production. Vigorous plants that have not been weakened by overgrazing produce a large yield of forage and a viable seed crop

which matures fairly early. Plants seriously weakened by overgrazing produce but little forage and usually fail to develop any seed.[432] Grazing a pasture to its maximum capacity year after year invariably results in a sharp decline in its carrying capacity, *i.e.* the number of stock it can support. Until a study of indicators of overgrazing was made, judgment as to the condition of the pasture was based on general observations, such as the abundance and luxuriance of the plant cover as a whole and the condition of the grazing animals. Unfortunately, until the plant cover had been greatly disturbed or a large proportion of the more valuable species actually killed, deterioration was not recognized. When this stage of depletion has been reached, many seasons of proper management are required to reestablish the original forage cover.

Definite successions occur in pastures and on range lands, as has been clearly recognized. Before the ranges were overgrazed, the grasses of the red prairies of Texas were largely bluestems (*Andropogon*), often as high as a horse's back. After pasturing and subsequent to the trampling and hardening of the soil, the wire grasses (*Aristida*) spread over the whole country. After further overstocking and trampling, the wire grasses were driven out and mesquite grass (*Hilaria*) and buffalo grass (*Bulbilis*) became the most prominent species. The occurrence of any one of these as the dominant is, to some extent, an index of the state of the land and of the stage of overstocking and deterioration that has been reached.[497]

When the enormous herds of buffaloes roamed the prairies of eastern Kansas and Nebraska, the tall grasses were closely eaten and much trampled. The prairies, moreover, were repeatedly burned. Burning and trampling were distinctly more favorable to the short, buffalo and grama grasses than to their tall-grass competitors. The westward movement of the buffalo and their decrease in numbers coincided with the incoming of the settlers and the decrease in prairie fires. This resulted in the renewed growth of the tall grasses and the gradual shading out of the buffalo and grama grasses. It explains the belief of the pioneers that the bluestems (*Andropogon*) followed in the wake of the settlers and drove out the buffalo grass.

Degree of Overgrazing.—The degree of overgrazing is shown by two types of indicators—those due primarily to the fact that they are not eaten, and those that invade because of disturbance. The more palatable species are eaten down, thus rendering the uneaten ones more conspicuous. This quickly throws the advantage in competition to the side of the latter. Because of more water and light, their growth is greatly increased. They are enabled to store more food in their propagative organs as well as to produce more seed. The grazed species are correspondingly handicapped in all these respects by the increase of less palatable species and the grasses are further weakened by trampling as stock wanders about in search of food. Soon bare spots appear that are

colonized by weeds or weed-like species. The weeds reproduce vigorously and sooner or later come to occupy most of the space between the fragments of the original vegetation. Before this condition is reached, usually the stock are forced to eat the less palatable species, and these begin to yield to the competition of annuals. If grazing is sufficiently severe, these, too, may disappear unless they are woody, wholly unpalatable, or protected by spines.

Signs of Overgrazing.—There are several conspicuous signs of overgrazing, some or all of which may be observed in many pastures, for overgrazing or trampling for a period will produce indicators that may

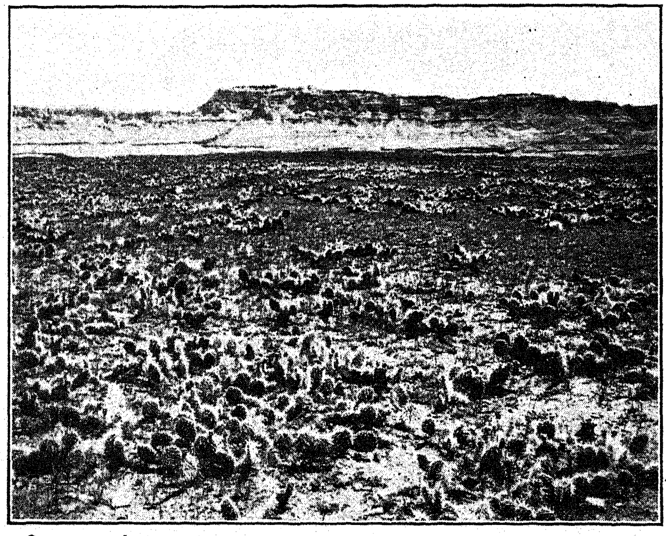

FIG. 239.—Overgrazed range in western Nebraska indicated by the abundance of cactus (*Opuntia*).

readily be recognized. Obviously, these indicators are not the same in all parts of the United States, but once the underlying principles of overgrazing are comprehended, a little study will reveal them anywhere (Fig. 239).

The predominance of annual weeds and short-lived, unpalatable perennials indicates severe overgrazing and characterizes pastures in advanced stages of depletion. Prominent among these are knotgrass (*Polygonum*), lamb's-quarters (*Chenopodium*), tansy mustard (*Sophia*), annual brome grasses (*Bromus tectorum, B. hordeaceus*), peppergrass (*Lepidium*), squirrel-tail (*Hordeum jubatum*), etc. Characteristic species representing a less pronounced degree of overgrazing are gum weed (*Grindelia*), yarrow (*Achillea*), ironweed (*Vernonia*), vervain (*Verbena*), thistle (*Carduus*), goldenrod (*Solidago*), abundance of cactus (*Opuntia*), etc. (Fig. 240). Early indicators of range deterioration are a decrease

in abundance of the more valuable species of grasses, such as needle grasses (*Stipa*) and wheat grasses (*Agropyron*) in prairie; an increase in the less valuable ones, *e.g.* wire grass (*Aristida*), accompanied by an increase in the short grasses (*Bouteloua, Bulbilis*) where they are associated with the taller ones. This is followed or accompanied by a marked increase in vigor and abundance of societies, such as sages (*Artemisia*), goldenrods (*Solidago*), asters, various legumes (*Astragalus, Lupinus, Amorpha*), etc.

Thus, the species that are increasing on an area reveal one of two things. If they represent stages earlier in the successional development than that of the predominating vegetation when the range is at its highest

FIG. 240.—Gum weed (*Grindelia*) and ironweed (*Vernonia*) in an overgrazed pasture.

efficiency, the area is being misused and its carrying capacity is decreasing. If, on the contrary, the species for grazing that are increasing are those of the climax stage or at least higher than the original vegetation as a whole, the plan of grazing is satisfactory. In the former case, proper remedial measures such as reducing the number of stock, deferring grazing until the more important species have produced flower stalks and seeded, etc., will initiate a succession that will again culminate in the climax vegetation. In humid climates, especially, this may often be hastened by artificial seeding.

Other signs of overgrazing, especially in forest and scrub, consist of damage to tree reproduction, *e.g.* yellow pine, aspen, etc.; remnants of dead shoots of palatable woody plants such as coralberry (*Symphoricarpos*), service berry (*Amelanchier*), willow (*Salix*), etc.; and, everywhere in general, erosion, roots of vegetation exposed by trampling, bare soil, and deeply cut trails where formerly the cover of vegetation was intact.

To Study the Degree of Overgrazing.—Visit a number of pastures and make a careful examination for indicators of overgrazing. Compare the vegetation about gates, watering troughs, or shade trees where the animals collect and trample the grasses with that of the pasture generally. Try to determine the past history of the pasture and, if possible, the original type of vegetation. Do the different pastures show the same degree of overgrazing? What are the most important indicators of disturbance? Are the indicators different in pastures for cattle or horses and sheep or hogs? Which shows the greatest disturbance and why? What remedial measures would you suggest?

INDICATORS OF FOREST

Forest indicators are of three chief types, namely, those that have to do with existing forests, those that indicate former forests, and those that indicate the possibility of establishing new forests. Obviously, every forest climax indicates a forest climate although of different degrees. The deciduous forest indicates one with long, hot summers and moderately cold winters with an abundance of both summer and winter precipitation. The three Rocky Mountain climaxes, *viz.* woodland (*Pinus-Juniperus*), montane (*Pinus-Pseudotsuga*), and subalpine forest (*Picea-Abies*) indicate climates with a progressive increase in rainfall and corresponding decrease in temperature and length of growing season. The forest formation that is the climax for a region indicates the type of forest that will naturally develop or redevelop in all bare or cleared areas. The various groupings of species and the differences in density and growth of dominants and subdominants serve to indicate differences in edaphic conditions and minor changes in the factor complex. Seral communities likewise indicate differences in edaphic conditions or habitats. They often indicate the nature of the original area (whether wet or dry) or the nature of the disturbance (such as fire, wind throw, lumbering, etc.) and the particular stage in the development of the succession.

Indicators of Former Forests.—Such indicators are either actual relicts of the forest itself or seral communities that mark particular stages of succession toward reforestation. Brush or scrub are characteristic indicators of fire in forest regions. Aspen (*Populus tremuloides*) and birch (*Betula*) are typical indicators of fire in forest communities throughout boreal North America as well as in many mountainous regions. This is due to their ability to form root sprouts, and the trees often occur in groups as a consequence (Fig. 241). Among certain species of pines, the cones remain closed upon the branches for many years but open readily after fire, thus furnishing a large number of seeds for immediate germination. Three important species of this type occur in western North America, namely, lodgepole pine (*Pinus contorta murrayana*), jack pine (*P. banksiana*), and knobcone pine (*P. attenuata*). These are all typical indicators of burns and form subclimaxes of great extent and duration in areas frequently swept by fire.

After the forest cover has disappeared because of fire, lumbering, lack of reproduction due to overgrazing, or other factors, the area is freed from the competition of climax species and conditions made favorable for the growth of many subdominants. As a result of excessive seed production, the ability to produce root sprouts, or the opening of cones by fire, these rapidly and often completely occupy the ground. Fires of recent occurrence are indicated by an abundant growth of liverworts and mosses such as *Marchantia*, *Funaria*, and *Bryum*, which frequently cover the soil, and by characteristic annuals and perennials as fire grass (*Agrostis hiemalis*), fireweed (*Chamaenerion angustifolium*), everlasting

FIG. 241.—Reproduction of linden or basswood (*Tilia americana*) by sprouts after cutting.

(*Anaphalis margaritacea*), thistles (*Carduus*), milfoil (*Achillea*), bracken (*Pteris aquilina*), and other species with wind-blown propagules. Burns of greater age are characterized by various shrubs that have developed from root sprouts. Raspberry (*Rubus strigosus*), hazelnut (*Corylus americana*), and huckleberry (*Vaccinium macrophyllum*) are characteristic species. The number and distinctness of these seral communities and their duration depend chiefly upon the severity of the burn. In the western forests the shrubs are normally replaced by aspen, birch, or alder, which later give way to subclimax or climax forest. In the cedar-hemlock forests of the Pacific Northwest, Douglas fir, the most valuable of lumber trees, forms a remarkably permanent subclimax over an enormous extent due to repeated burns.

Such seral communities not only indicate the possibility of reforestation, but they also make it clear that artificial means, such as periodic

removal of the forest, must be resorted to where it is desirable to maintain the subclimax as a relatively permanent type.

Planting Indicators.—Indicators of sites for planting are of two kinds, namely, those that indicate the former presence of a forest, and those that suggest the possibility of developing forest in grassland or scrub areas. These are indicators of reforestation and afforestation, respectively.[291]

The obvious indicators of reforestation are relict survivors, or trunks and stumps. Charred fragments of wood or pieces of charcoal in the soil are less obvious but equally conclusive. Where there is no direct evidence of the original forests, indirect evidence is often furnished by indicator communities which bear a direct relation to forest. Such are seral and subclimax communities that show a successional relation to the forest climax and societies of shrubs or herbs which formed layers in them. Thus, areas of coralberry (*Symphoricarpos*) or prickly ash (*Zanthoxylum*) with societies of Solomon's-seal (*Polygonatum*), bloodroot (*Sanguinaria*), and similar mesophytic herbs indicate former forest lands.

Indicators of afforestation are either savannah, *i.e.* isolated trees or clumps of trees in grassland, chaparral, or tall-grass prairies in which the water requirements are very near those of trees, such as subclimax prairie.

The indicators of sites for planting or sowing serve also to indicate the preferred species. In reforestation, for example, the general rule is to employ the species of climax trees that were in possession, unless reasons of management may make it desirable to employ a subclimax dominant. Species somewhere in contact with grassland or scrub give the clue to the selection of those best adapted for afforestation. Thus, yellow pine from the foothills has been successfully grown in the grass-covered sandhills of Nebraska and is also one of the best species for planting in loam soils.

Where the virgin timber has nearly or altogether disappeared, as a result both of severe burns and of grazing, and has been replaced by shrubs, herbaceous vegetation, and wide stretches of aspen extending over an area originally occupied by several forest types, the question of deciding what species to plant on a given site becomes very difficult. But even in such cases a study of the existing vegetation furnishes the most valuable guide, as has been repeatedly demonstrated in forest practice.[604]

Thus far, practical afforestation has been confined chiefly to the sandhills of Nebraska and Kansas, although conditions for afforestation have been carefully studied in the Great Basin.[25,83] In Nebraska, where afforestation has been successful, four indicators of its possibility are present.[499] These consist of valley and canyon relicts of woodland (both deciduous and evergreen); a savannah-like growth in contiguous

uplands (principally of western yellow pine); shrubs that show a close approach to the water requirement of trees (*viz.* sand cherry, willow, hackberry, wild plum); and tall grasses, (*Andropogon*, etc.) indicating similar water relations. In Kansas, where afforestation failed, these indicators were largely lacking.

LAND CLASSIFICATION

The classification of land is an endeavor to forecast the type of utilization that will yield adequate or maximum returns.[467] The natural plant cover is a result of all the growing conditions where it is produced. It is an index or measure of the factors influencing its growth and serves as an indicator of the possibilities of producing other plants on the land. Consequently, it is invaluable in classifying lands in regard to their suitability for agriculture, grazing, or forestry. If agriculture is possible, indicators may be used to denote the greater feasibility of humid, dry, or irrigation farming or the importance of combining grazing with dry farming. Where grazing is concerned, the type of vegetation determines whether cattle, sheep, or goats are preferable or a combination of two or three. Similarly, the vegetation may be employed to determine the possibility of afforestation or reforestation as well as the most promising dominants for any particular region.

During the last 20 or 30 years, the large majority of homesteads taken have proved failures, and the percentage of failures will steadily increase as still less promising regions are entered, unless adequate knowledge of the potentialities of the lands is to be had. Consequently, all the principal types of vegetation occurring on the unreserved public lands and the patented homestead lands west of the one hundredth meridian have been classified with special reference to their suitability for grain farming, forage production, or grazing. The relative carrying capacity of the different types of grazing lands has, moreover, been determined. A total of 102 types of vegetation are used as illustrated by the following:

Sagebrush (*Artemisia tridentata*).—The sagebrush type consists of a miniature forest or scattered brush land of sagebrush. Plants vary in height from 1 to 7 feet. This is the most common shrub throughout the Great Basin, growing in well-drained loamy soils. The height and abundance of plants are governed by the depth, quality, and moisture content of the soil. A dense stand of tall sagebrush is indicative of very favorable possibilities for the production of small grains without irrigation. It represents the best type of land in the Great Basin for farming, either arid or by irrigation. This type is grazed by stock, mainly sheep, during fall and winter when little or no herbaceous feed is available.

Mesquite (*Prosopis*).—Areas supporting little or no vegetative growth other than mesquite are classified in this type (Fig. 242). This shrub varies in size from only a few feet to trees 30 feet high. It occupies a large acreage in southern New Mexico and Arizona and has considerable economic value for the stock feed

supplied from the leaves and beans. The roots and the thicker stems also supply considerable fuel. It is very common in deep fertile soil along drainage channels where subirrigation is usually received. The better types of this land are capable of producing forage crops such as sorghums, corn, and millet, during very favorable years. It has a carrying capacity of 5 to 15 head of cattle per section.

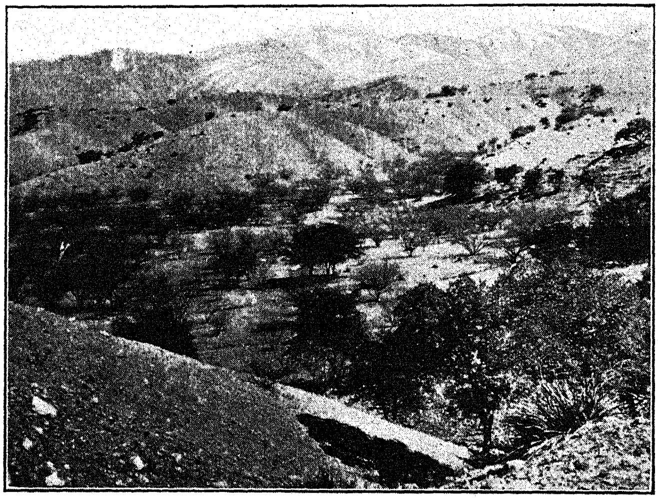

FIG. 242.—Mesquite (*Prosopis*), a leguminous tree growing in Arizona and the arid Southwest.

Coeosote Bush (*Larrea*) **and Cacti** (*Opuntia* spp.).—This type grows in rather broken or rocky areas in southern New Mexico and the desert regions of Arizona, southern Nevada, and southeastern California. It is made up of a scattered growth of creosote bush and an abundance of cacti, especially the barrel cactus which varies in diameter from 1 to 1.5 feet, and in height from 2 to 4 feet; and the round-stemmed opuntias, especially the dense spiny *Opuntia spinosior*. It is non-agricultural unless irrigated and of little or no value for grazing.[7]

Similar classifications, perhaps refined by quantitative methods and increasing experience, must sooner or later be used in all new regions of the world where maximum economic returns are desired.

CHAPTER XVIII

CLIMAX FORMATIONS OF NORTH AMERICA

Nature of Climaxes.—An airplane view of the continent of North America would reveal the fact that it is covered by three great types of vegetation, namely, forest, scrub, and grassland. A closer scrutiny would disclose that these are themselves composed of strikingly different communities, such as evergreen and deciduous forest, which are found in climates equally different. These units, of vast extent and great permanence, are termed climaxes or formations; they are the product of climate and, hence, are controlled by it. Each formation is the highest type of vegetation possible under its particular climate, and this relation makes the term *climax* especially significant, as it is derived from the same root as *climate*. The formation and climax are identical, and, hence, the same great community may be termed a formation, a climax or, for the sake of emphasis, a climax formation.

Each climax owes its characteristic appearance to the species or dominants that control it. These dominants exhibit the same vegetation- or life-form—tree, shrub, or grass, as the case may be—and thus serve to give to the climax the imprint of its climate. The dominants all belong to the highest type of life-form possible under the prevailing climate; in forest they are all trees of the same type, in grassland all grasses or sedges, and so forth. It is necessary, however, to distinguish plants that are merely conspicuous or abundant from those that are actually dominant. This is particularly true of the various savannah communities, in which the trees and shrubs are much more conspicuous than the grasses, but the latter are in actual control of the habitat. In the subclimax and true prairies, the dominant grasses are more or less concealed during the growing season by tall forbs,* such as *Erigeron*, *Psoralea*, and *Solidago*. These are termed *subdominants* and constitute seasonal societies subject, in large measure, to the control of the grasses.

Animals also play an important part in the climax and are intrinsic members of the community along with the plants. They are not dominants, since they are not directly responsive to the climate in the way that plants are and they exert little or no controlling reaction upon the habitat. Their presence and abundance are determined, in the first instance, by the plant dominants, and, like the forbs, animals could be regarded as subdominants. For a number of reasons, it is more con-

* The term *forb* is used to denote herbs other than grasses.

venient to employ a distinct term and call them *predominants* in reference to their abundance and corresponding importance. Their significance and rôle in the climax are likewise determined by the life-form, which finds its primary expression in the food coactions.

Before the advent of civilized man, nearly the whole area of each climax was occupied by the dominant species. The exceptions were the numerous but relatively small and scattered portions in which succession was taking place in primary areas of water, dune sand, or rock. With the opening of the historical period came a great increase in the destruction of natural communities by fire, lumbering, and clearing for cultivation. Such effects stand in the closest relation to the period of settlement and the intensity of human coactions and have led to the all but complete disappearance of the climax in regions long cultivated. Nevertheless, all areas within the sweep of climate and climax, whether bare or denuded by man, are marked by a more or less evident successional movement of communities and, hence, belong to the climax in terms of its development. In consequence, each climax consists not merely of the stable portions that represent its original mass but also of all successional areas, regardless of the kind or stage of development.

Tests of a Climax.—Each climax is the direct expression of its climate; the climate is the cause, the climax the effect, which, in its turn, reacts upon the climate. So intimate is this relation that the climax must be regarded as the final test of a climate rather than human response or physical measurements. Climates are to be recognized and delimited by means of their climaxes and not the reverse, not merely on account of the cause-and-effect relation but also by virtue of the fact that the effect is much more visible and less variable than the cause. No matter how complete his equipment of meteorological instruments, the ecologist must subordinate such measures of climate to the judgment of the plant community, if his results are to be both accurate and usable. The paramount importance of formations and associations in indicating climates makes their objective recognition of the first importance, and for this purpose a number of guiding principles have been established.

The first criterion is that all the climax dominants must belong to the same major life-form, since this indicates a similar response to climate and, hence, a long association with each other. Neither forbs nor woody plants are to be considered as dominants in grassland, nor are evergreen trees proper dominants of deciduous forest. The second principle is that one or more of the dominant species must range throughout the formation or occur in the various associations to some degree. This is exemplified in the prairie climax by *Stipa comata*, *Bouteloua gracilis*, and *Agropyron smithii* and in the deciduous forest by *Quercus rubra* and *macrocarpa*. The third criterion is that a large number and usually the majority of the dominant genera extend throughout the formation, though

represented by different species. This is true of *Stipa*, *Bouteloua*, *Andropogon*, *Agropyron*, *Poa*, and *Sporobolus* in the grassland, and of *Quercus*, *Hicoria*, *Acer*, *Tilia*, and *Betula* in the deciduous forest and of *Pinus*, *Picea*, and *Abies* in the coniferous forests.

A fourth principle is derived from the degree of equivalence exhibited by the dominants of two contiguous associations where they meet in the ecotone between the two. The existence of such a transition area over a wide stretch indicates that the dominants are sufficiently alike to belong in the same formation but dissimilar enough to characterize different associations. A fifth deals with the relation of the various associations to subclimaxes or subclimax species. Thus, in the grassland climax, the several species of *Andropogon* are subclimax to four of the associations, and occasional relicts suggest that they were formerly in the case of the other two. *Ulmus*, *Fraxinus*, and *Acer* bear a similar relation to the three associations of the deciduous forest. This principle applies likewise to relict areas of adjacent formations, such as the preclimaxes and postclimaxes discussed in the next section. The sixth criterion arises out of the evolution and relationship of formations and the phylogenetic comparison of similar formations in the two hemispheres. As in the case of genera and species, formations have arisen from the modification of earlier ones, just as associations have been produced by the differentiation of formations under the compulsion of climatic changes. In fact, it is most probable that the modifying action of climatic cycles has been exerted simultaneously upon both community and species.

Preclimax and Postclimax.—A subclimax arises when the course of succession is halted for a long period in the stage just preceding the climax or, more rarely, in the next earlier stage. The most frequent and striking examples are the result of repeated fire; as the list of formations shows, practically every coniferous climax exhibits a fire subclimax of so-called jack pines, usually species with closed and persistent cones. Boreal and mountain forests are everywhere interspersed with subclimaxes of aspen, paper birch, or both, while overgrazed mixed prairie yields to a community of short grasses. The subfinal stage in succession regularly persists likewise when the reaction of the community is constantly compensated by physiographic processes, as in flood plains and valleys, and in dunes and sandhills. Practically everywhere the vegetation of river valleys is subclimax to that of the country roundabout, and a similar relation is to be found upon rocky slopes or in sandy stretches through all formations.

All the formations of a continent stand in a definite climatic relation to each other, best seen in miniature on the slopes of a high mountain range. An effective change in climate will cause each one to replace the next but without disturbing their essential arrangement. A shift in the direction of greater rainfall will permit the more mesophytic to

replace the less mesophytic throughout the series, while a swing toward less rainfall will favor the more xerophytic community at each line of contact. As a consequence, each formation or association plays a double rôle. It is a preclimax to its more mesophytic neighbor and a postclimax to its more xerophytic one, though under the fairly static conditions of a major climatic phase the movement is only a potential one. The great climatic changes of the past, however, have everywhere left relict communities that bear one relation or the other to the surrounding climax of the present day. The oak-chestnut association of the deciduous forest formation is climatically intermediate to the preclimax oak-hickory on the one hand and the postclimax maple-beech on the other. This is not only the general climatic relation of the three communities of this formation, but it is also the actual physiographic arrangement. In its own subclimate, the oak-chestnut is the prevalent type, with preclimax oak-hickory wherever slope exposure, soil, or local rainfall reduces the effectiveness of the water content and with postclimax maple-beech or ash-elm where the water relations are most favorable. In the grassland climax, the short grasses constitute preclimax communities far into the true and subclimax prairie with much higher rainfall, and the bluestems extend more or less throughout mixed prairie and desert plains as postclimax relicts in a rainfall but a third as great as that of the subclimax prairie of the Mississippi Valley. This prairie is itself a preclimax to the deciduous forest with higher rainfall, and it undoubtedly represents a wedge driven into the forest region by a major dry phase of the climatic cycle.

Classification.—The formations of a continent may be grouped in several ways in accordance with the emphasis placed upon the various criteria. Perhaps the simplest classification is that based upon geographic position, which necessarily reflects climatic relations in some degree. The most definite is probably the grouping, upon the basis of life-form, into forest, scrub, and grassland. The causal relation is best shown when climate is fully taken into account, but this leads to the difficulty found in the fact that the climaxes are themselves the best indicators of climate. The most fundamental and, hence, the most natural classification is grounded upon evolution and relationship, as in the case of species and genera. This, furthermore, possesses the great advantage of including the other criteria to the extent that they are important and thus leads to a natural system that is both comprehensive and objective. It is evident that such a classification depends upon thoroughgoing investigation in the field, of both the intensive and extensive kind, and that it must ultimately deal with more than one continent. The following grouping makes use of life-form and climate for the primary divisions, but the arrangement of climaxes within these is as natural as the consideration of a single continent permits.

LIST OF FORMATIONS AND ASSOCIATIONS

Tundra Climax:

Tundra: Carex-Poa Formation

1. Arctic tundra: Carex-Cladonia association
2. Petran tundra: Carex-Poa association
3. Sierran tundra: Carex-Agrostis association

Forest Climaxes:

Boreal Forest: Picea-Larix Formation

1. Spruce-larch forest: Picea-Larix association
   a. Birch-aspen subclimax: Betula-Populus associes
2. Spruce-pine forest: Picea-Pinus association

Subalpine Forest: Picea-Abies Formation

1. Petran subalpine forest: Picea-Abies association
   a. Lodgepole subclimax: Pinus consocies
2. Sierran subalpine forest: Pinus-Tsuga association

Lake Forest: Pinus-Tsuga Formation

1. Pine-hemlock forest: Pinus-Tsuga association
   a. Jack-pine subclimax: Pinus consocies

Coast Forest: Thuja-Tsuga Formation

1. Cedar-hemlock forest: Thuja-Tsuga association
   a. Douglas-fir subclimax: Pseudotsuga consocies
2. Larch-pine forest: Larix-Pinus association

Montane Forest: Pinus-Pseudotsuga Formation

1. Petran montane forest: Pinus-Pseudotsuga association
2. Sierran montane forest: Pinus-Abies association

Deciduous Forest: Quercus-Fagus Formation

1. Maple-beech forest: Acer-Fagus association
2. Oak-chestnut forest: Quercus-Castanea association
3. Oak-hickory forest: Quercus-Hicoria association
   a. Pine subclimax: Pinus associes

Grassland Climax:

Prairie: Stipa-Bouteloua Formation

1. True prairie: Stipa-Sporobolus association
   a. Subclimax prairie: Andropogon associes
2. Coastal prairie: Stipa-Andropogon association
3. Mixed prairie: Stipa-Bouteloua association
   a. Short-grass plains: Bulbilis-Bouteloua associes
4. Desert plains: Aristida-Bouteloua association
5. Pacific prairie: Stipa-Poa association
6. Palouse prairie: Agropyron-Festuca association

Woodland Climax:

Woodland: Pinus-Juniperus Formation

1. Piñon-juniper woodland: Pinus-Juniperus association
2. Oak-juniper woodland: Quercus-Juniperus association
3. Pine-oak woodland: Pinus-Quercus association.

Scrub Climaxes:

Chaparral: Quercus-Ceanothus Formation

1. Petran chaparral: Cercocarpus-Quercus association
   a. Oak-sumac subclimax: Quercus-Rhus associes
2. Coastal chaparral: Adenostoma-Ceanothus association

Sagebrush: Atriplex-Artemisia Formation

1. Basin sagebrush: Atriplex-Artemisia association
2. Coastal sagebrush: Salvia-Artemisia association

Desert Scrub: Larrea-Franseria Formation
1. Desert scrub: Larrea-Franseria association
   a. Bronze scrub: Larrea-Flourensia associes
   b. Mesquite: Acacia-Prosopis associes
   c. Sotol: Agave-Dasylirion associes
   d. Thorn scrub: Cereus-Fouquiera associes

Tropical Climaxes.

TUNDRA CLIMAX

The Tundra

Extent and Nature.—The tundra stretches from the Atlantic to the Pacific Ocean, occupying the broad zone between the tree limit and the region of perpetual snow about the north pole. The main body reaches farthest south as narrow belts along cold bodies of water such as Hudson Bay and the Labrador Current, but as alpine tundra this climax occurs on high mountains southward into Mexico and reappears with its composition much modified on the Andes of South America. Throughout this vast range it is characterized by the grass life-form, together with a host of perennial forbs belonging largely to the same genera of northern origin. In consequence of low temperatures, short seasons, and drying winds, the plants are typically dwarfed, the dense sward often rising but a few inches above the level of the soil. The season is short, often lasting but 2 months, and frost or freezing may occur at any time during the growing period, especially at night. The precipitation varies greatly, being highest in coastal regions, but evaporation and transpiration are marked, and the water content correspondingly decisive. The light relations are unique, both in the Arctic where day and night divide the year, and on alpine summits where the blue and ultra-violet rays are stronger than at low altitudes.

Practically throughout the Northern Hemisphere, the tundra lies in contact with a boreal or subalpine forest of fir, spruce, and their associates. The component species naturally differ from Europe and Asia to Arctic America and to the Cordilleras of the United States and Mexico, much as they do in the tundra climax itself. The latter, however, lives under uniform and rigorous conditions, and, in consequence, an exceptionally large number of species occur more or less throughout it. The tundra of northern Europe and Siberia is remarkably like that of North America and it is only between Arctic and alpine tundra that considerable differences are found. In the present knowledge of this vegetation, two formations can be distinguished, one Eurasian, the other American, and both of these can be further divided into Arctic and alpine associations.

The alpine areas represent relict communities that were left behind as the main mass of the tundra retreated in the wake of melting glaciers. The three great mountain systems of the continent furnished a haven for Arctic species to a degree determined chiefly by elevation and extent. In

the East, they persisted only on a few isolated peaks such as Mount Washington and Mount Katahdin, which lie only a few hundred miles south of the present limits of Arctic tundra. In the Sierra Nevada, alpine tundra occurs a thousand miles southward of the Arctic, while in the main Cordilleras it reaches 2,000 miles into the Sierra Madre of Mexico. As a consequence, it has been found desirable to recognize three associations, namely: (1) Arctic tundra, which may well include the alpine communities of New England; (2) Petran tundra, found in the Rocky Mountains; and (3) Sierran tundra, confined to the Sierra Nevada and Cascade Mountains.

Arctic Tundra.—As already indicated, this constitutes the great mass of the tundra climax and, with the exception of the small rearguards in

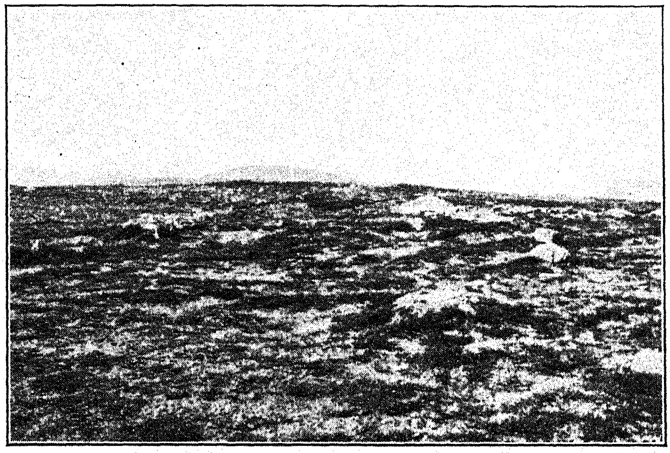

FIG. 243.—Arctic tundra of wind-eroded *Empetrum* and *Betula nana* heather rich in lichens (*Photo by H. Smith, Upsala; by courtesy of Dr. DuRietz.*)

New England, is confined entirely to the Arctic regions. It follows the coast as a solid and usually broad band from the Alaskan peninsula to Newfoundland, covering the islands of the Arctic archipelago but only the coastal fringe of Greenland. It occupies the mountain ranges and elevated plateaus of the interior, where it is much interrupted by the boreal forest (Frontispiece).

The tundra climax consists chiefly of four communities the successional relations of which are little understood as yet. It seems probable that the climax proper is represented by an association of sedges, grasses, and forbs, much interrupted by subclimaxes and forming various mixtures with them (Fig. 243). The cotton-grass bogs are to be regarded as the subclimax of the hydrosere, the heath moors probably as postclimax, and the lichen-moss tundra as the subclimax of the xerosere or as a preclimax. The dominants of the climax association are various species of *Carex*, such as *rigida*, *rupestris*, *incurva*, etc., *Luzula spicata* and *nivalis*, and a large number of grasses, *viz. Agrostis*, *Aira*, *Alopecurus*, *Arcta-*

grostis, *Calamagrostis*, *Danthonia*, *Festuca*, *Phleum*, *Poa*, and *Trisetum*. The moister or more open climax areas, as well as the subclimax ones, are brightened by a host of perennial forbs, which are much reduced in number where the competition of the sedges and grasses is severe. These subdominants occur mostly in mixed societies, which characterize two aspects, one early in July and the other in late July and August. The genera of chief importance are the following: *Anemone*, *Caltha*, *Ranunculus*, *Dryas*, *Geum*, *Potentilla*, *Astragalus*, *Lupinus*, *Saxifraga*, *Papaver*, *Draba*, *Cerastium*, *Lychnis*, *Silene*, *Androsace*, *Dodecatheon*, *Primula*, *Oxyria*, *Gentiana*, *Polemonium*, *Myosotis*, *Castilleja*, *Pedicularis*, *Achillea*, *Arnica*, *Artemisia*, *Senecio*, and *Lloydia*. All of these appear also as subdominants in the alpine tundra, though the number of species in some genera is reduced.

The submerged stage of the hydrosere is represented chiefly by *Hippuris vulgaris*, *Ranunculus purshii*, and *Sphagnum fuscum*, and the amphibious one by *Caltha palustris radicans*, *Ranunculus pallasi*, *Cardamine pratensis*, *Eriophorum scheuchzeri*, *Equisctum variegatum*, and many species of *Carex*. The drier swamps contain *Senecio palustris*, *Pedicularis sudetica*, *Polygonum bistorta*, *Potentilla palustris*, *Saxifraga hirculus*, etc., together with other species of *Carex* and *Eriophorum*. The pioneers on sand dunes are *Elymus arenarius*, *Artemisia comata*, *Epilobium latifolium*, *Helianthus peploides*, etc., while *Mertensia maritima*, *Cerastium alpinum*, *Polemonium boreale*, *Alopecurus alpinus*, and others grow on the more stable beach. The transition to the tundra is effected by *Festuca ovina*, *Luzula nivalis*, *Oxyria digyna*, *Papaver nudicaule*, *Draba*, *Senecio*, *Dryas*, *Primula*, and many species of *Saxifraga*.

The postclimax of heaths and of willows and birches, often much mixed, occurs on rich, moist soils or on protected slopes and in valleys; the heath moor, in particular, often represents a late stage of the *Sphagnum* bog. The dominants are *Cassiope tetragone*, *Empetrum nigrum*, *Andromeda polifolia*, *Arctostaphylos alpina*, *Ledum palustre*, *Rhododendron lapponicum*, *Rubus chamæmorus*, *Loiseleuria procumbens*, *Alnus sinuata*, several species of *Vaccinium* and *Betula*, and many of *Salix*. The preclimax of mosses and lichens consists principally of species of *Sphagnum*, *Dicranum*, and *Polytrichum* and of *Stereocaulon*, *Alectoria*, *Cetraria*, and *Cladonia*. The latter exhibits by far the greatest number of species, the largest life-forms, and greatest abundance, the dominant species of the first importance being *Cladonia silvatica* and *rangiferina*. The lichen carpet attains an average height of 4 to 5 and a maximum of 10 inches and under such conditions simulates a climax more or less closely.[265,379]

Petran Tundra.—The alpine tundra of the Rocky Mountains finds its best expression between 11,000 and 14,000 feet, though it is progressively lower to the northward and is also depressed by stream ways and lake

basins. The northern limit is in central Alberta, where it comes in contact with Sierran tundra, and the southern on the high peaks of New Mexico and northern Arizona. The general western limit is in Utah and Idaho, though relicts of this community are also to be found in the mountain ranges of Nevada. Much the largest part of the association is found in the extensive alpine zone of Colorado, but considerable areas occur in New Mexico, Utah, and Wyoming. At its lower edge the alpine tundra lies in contact with the subalpine forest, while above it reaches to the summit of the highest peaks (14,500 feet), though greatly reduced in species and dominance.[91]

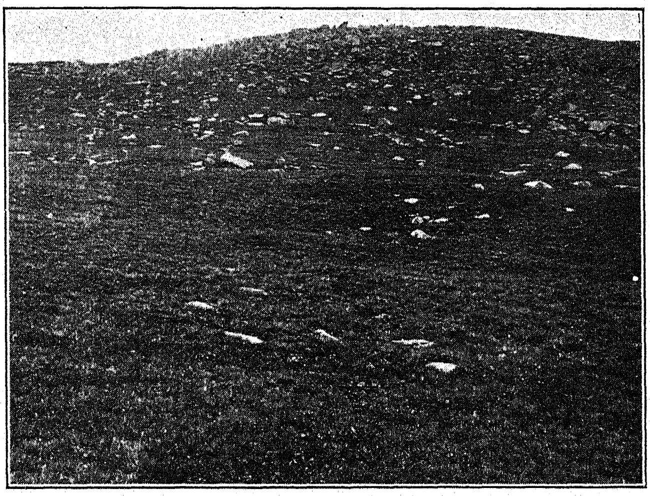

FIG. 244.—Petran alpine tundra, *Carex-Poa* association, Pike's Peak.

The number of dominants in this association is very large, though the leading rôle is assumed by a relatively small group. The typically climax condition is constituted by the sod-forming or densely bunched sedges, especially *Elyna bellardi, Carex rupestris, filifolia, pyrenaica, nigricans, nardina,* etc. The grasses are of less importance, though they play a considerable part but more particularly in the subclimax communities. *Poa* exceeds all others in the number of species, but *Agrostis, Aira, Danthonia, Festuca, Phleum, Trisetum,* and the grass-like *Luzula* are represented by one or more species of distinct significance. All of the genera and many of the species are likewise present in the Arctic tundra (Fig. 244).

The number of subdominant forbs is very large, and, for the most part, they constitute mixed societies of several species. These mark three more or less well-defined aspects, namely, early, middle, and late summer. A large number of the species are endemic, while of a total of about 90, a third occur in the Sierran tundra also, another third in

the Arctic, and the same number in Eurasia. This uniformity in distribution is largely a coincidence, for the species are not the same throughout. The genera are, however, practically identical for the circumpolar region and the two mountain systems, the endemic species of the latter, as a rule, being recent and direct descendants of those of wide distribution.

In accordance with the rule, alpine societies are best developed in subclimax or disturbed areas, in which the control of the dominant sedges and grasses is not yet complete. In the ultimate consociation of *Elyna bellardi*, for example, the dominance of this sedge is so complete as practically to exclude all but a few individuals of the forbs that thrive in the more open communities of *Carex rupestris* and the grasses. The vernal aspect rules through late June and early July and consists chiefly of *Primula angustifolia*, *Androsace chamœjasme*, *Eritrichium argenteum*, and *Caltha leptosepala*, often with several species of *Ranunculus*, *Draba*, *Trifolium*, *Thalictrum alpinum*, and *Besseya alpina*. The summer aspect prevails during most of July and early August and is characterized by a larger number of species of somewhat taller stature. Chief among these are *Actinella grandiflora*, *Mertensia alpina*, *Polygonum bistorta* and *viviparum*, *Artemisia scopulorum*, *Polemonium confertum*, *Erigeron uniflorus*, *grandiflorus* and *compositus*, *Antennaria alpina*, *Allium acuminatum*, *Potentilla rubricaulis*, and *Carduus hookerianus*. The major dominants of the late summer are *Campanula rotundifolia alpina*, *Gentiana frigida*, *Castilleja pallida occidentalis*, *Solidago virgaurea nana*, *Haplopappus pygmœus*, *Pentstemon hallii*, *Senecio taraxacoides* and *fremontii*[108] (Fig. 159).

Sierran Tundra.—The alpine peaks of the Sierran climax are slightly higher than those of the Rocky Mountains, but the tundra is depressed by permanent snow caps of great size. In the northern ranges its best expression occurs at 8,000 to 11,000 feet, though in the mountains of the upper Columbia Basin it may descend as low as 6,000 feet. In the Sierra Nevada the alpine climax is best developed between 10,500 and 13,000 feet. In general, the oceanic climate raises the timber line and lowers the snow line, with the consequence that the Sierran tundra is usually much less massive than the Petran. At its northern edge this association passes over into the Arctic tundra, while in the mountains of Montana and Alberta it merges with the Petran climax. It reaches its southern limit on San Jacinto Mountain, where it is represented by only a half-dozen relict species.

As in the other two associations, sedges constitute the chief dominants of the Sierran tundra, with *Poa*, *Agrostis*, and *Calamagrostis* next in importance, followed by *Trisetum*, *Festuca*, and *Luzula*. While the subdominants are much the same as in the Rocky Mountains, the most important ones belong to different species, though these, in turn, vary much from north to south. The much higher precipitation promotes

growth, and the forbs, in particular, are often much less dwarfed than in the Petran tundra, resembling the meadows of the latter. On such peaks as Mount Rainier, the spring aspect consists chiefly of *Erythronium montanum* and *parviflorum*, which appear as rapidly as the snow melts and even push through the snow banks themselves. The midsummer aspect comprises species of *Lupinus*, *Castilleja*, and *Erigeron*, together with *Potentilla*, *Polygonum*, *Valeriana*, etc.

FOREST CLIMAXES

The Boreal Forest

Extent and Nature.—Together with the tundra, the boreal forest possesses the distinction of stretching across the continent as a broad band, interrupted only by the tundra-covered mountains of the Yukon and Alaska. The climax dominants are conifers and chiefly evergreen, but they are more or less mixed with the subclimax aspens and birches throughout or replaced by them over considerable stretches. The northern boundary runs from the Mackenzie delta to the east of Great Bear and Great Slave lakes to Fort Churchill on Hudson Bay; it then swings around the bay to the northeast but reaches the coast only near Newfoundland, owing to the influence of the cold Labrador current. From Cook Inlet in Alaska the southern boundary trends southeastward to the aspen savannahs of Saskatchewan, eastward to Lake Winnipeg, and thence to northern New Brunswick (Frontispiece).

Although the climate is less severe than that of the tundra, it is still very rigorous, and through the northern third or more the trees are much reduced in stature and diameter. Over much of the vast region the trees do not leaf out before the first of June and the leaves fall early in September. The precipitation ranges from more than 40 inches in the east to less than 15 in the Yukon and is generally below 20 inches in the interior. The winters are long and severe; the snowfall is not excessive and the air is relatively dry. The ground is snow covered or frozen for nearly three-fourths of the year, and the subsoil is more or less permanently filled with frost. In general, the drainage is poor and the soils shallow and immature.[469]

As already noted, the boreal forest lies in contact with the Arctic tundra along its entire northern border, reaching the polar sea only at the Mackenzie Delta. It passes gradually into the Barren Grounds through a transition belt in which the timber steadily diminishes in stature and the species are reduced to two or three. Along the rivers this reduced forest may extend as much as 200 miles into the tundra, finally breaking up into isolated outposts. On the other hand, the tundra extends even farther southward into the forest along the low mountain ranges and on the plateaus, especially in Alaska and the Yukon.

In the southwest, this climax mixes with the subalpine forest in the Yukon and British Columbia and even with the northward extension of the coast forest in Alaska. One of its subclimax dominants extends well southward into the prairies of Alberta and Saskatchewan to form a characteristic belt of savannah.[310] From the region of the Great Lakes eastward the boreal forest has long been in contact with the pine forest and the deciduous forest. The repeated shiftings of the glacial period, together with the striking influence of lakes and rivers, have led to widespread alternation and mixing of the three climaxes, further complicated by fire and lumbering.

The boreal forest of North America has itself been differentiated from an earlier circumpolar mass and, hence, stands in close relationship to the coniferous forests of northern Europe and Siberia. It is even more closely related to the subalpine forests of the Rocky Mountains and the Sierran-Cascade system, which are to be regarded as more recent climatic modifications of it. The elevation of the Appalachians has been too slight to produce such a result, though the presence of *Picea mariana* and *Abies fraseri* in the southern ranges is evidence of such a tendency, which is further confirmed by the zone of boreal forest on the high peaks of New England.

Because of the general uniformity of conditions and their very gradual change to the north and west, this climax is not so distinctly marked off into associations. The disappearance of balsam fir, and jack pine, however, the increased importance of aspen and birch, and the entrance of alpine fir and lodgepole pine make the recognition of two associations necessary, though it must be admitted that the ecotone between them is a very broad one. The subclimax associes plays a much larger part than usual in most climaxes, owing to the fact that the subclimax dominants outnumber the climatic ones. Moreover, they not only take possession of fire-swept or lumbered areas but also assume a regular rôle in the succession found in the innumerable bogs and muskegs and on sandy or rocky plains.[221]

The Spruce-Larch Forest.—This association reaches from Labrador, Newfoundland, and New Brunswick on the east to the Rocky Mountains of northern British Columbia and the Yukon and in its extent across the continent is exceeded only by the Arctic tundra. In its strictest sense, its climax dominants are restricted to two species, the white spruce, *Picea canadensis* and the balsam fir, *Abies balsamea*, but the several subclimax trees may assume climax rôles as well. This is primarily an outcome of the climatic relations as the tree limit is approached, either in latitute or altitude. Increasingly rigorous conditions cause the climax species to dwindle in importance or drop out, while the less exacting ones persist. Thus, the larch or tamarack, *Larix laricina*, which is typical of bogs or muskegs through the heart of the forest, becomes essentially a

climax tree along the northern border (Fig. 245). This is likewise true of the paper birch, *Betula alba papyrifera*, which is elsewhere characteristic of burns or of immature soils. The black spruce, *Picea mariana*, grows commonly with larch in or about bogs, but it becomes climax on rocky plateaus or on high mountain slopes, and the aspen, *Populus tremuloides*, often exhibits the same tendency (Fig. 246). The jack pine, *Pinus banksiana*, appears to assume subclimax or climax rôles with equal readiness, but its definitely subclimax nature in the more temperate lake forest indicates that it is usually climax in the boreal one. The balsam poplar,

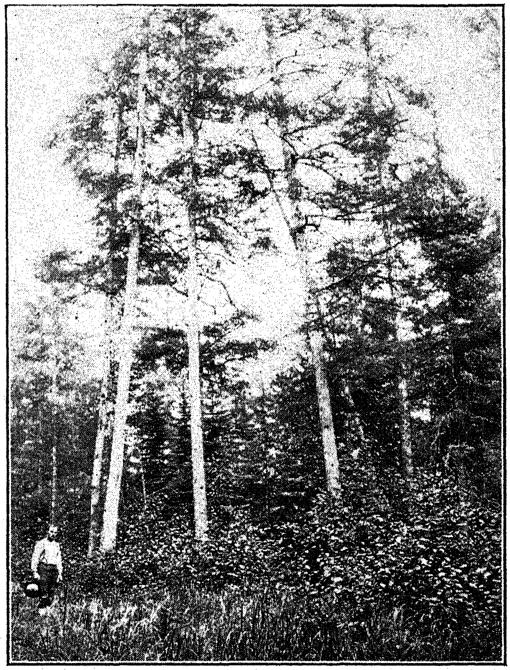

FIG. 245.—Mature tamarack (*Larix laricina*) in almost a pure stand and a few small black spruce (*Picea mariana*). (*Photo by courtesy U. S. Forest Service.*)

Populus balsamifera grandidentata, which is a true aspen, belongs in lowland or fire subclimaxes and is rarely if ever a climax species. Two other trees are frequent in the eastern portion of this association, namely, arborvitæ, *Thuja occidentalis*, and red maple, *Acer rubrum*. Both are more or less subclimax in nature, but they also persist well into the climax community. The former, however, is regarded as belonging properly to the lake forest and the latter probably to the deciduous one.

The characteristic undergrowth of the spruce-larch forest is supplied by the heath stage of the bog succession. The most important species are *Kalmia glauca* and *angustifolia*, *Ledum palustre* and *grœnlandicum*, *Chamœdaphne calyculata*, *Rhododendron canadense*, *Empetrum nigrum*,

Rubus chamæmorus, Andromeda polifolia, and several species of *Vaccinium: pennsylvanicum, cæspitosum, uliginosum, vitis-idæa, oxycoccus,* etc. Most of these grow taller and more open as the larch and spruce close in on the moor, and the least tolerant species drop out as the canopy thickens with the entrance of balsam and white spruce. The margins of the moor are occupied by taller species, such as *Alnus incana* or *crispa, Viburnum cassinoides* and *pauciflorum, Corylus rostrata, Cornus stolonifera, Pyrus arbutifolia, Myrica gale, Betula pumila, Spiræa salicifolia,* etc., and of these *Alnus, Corylus,* and *Spiræa* persist well into the shade.

FIG. 246.—Forest of black spruce (*Picea mariana*) in a muskeg covered with sphagnum. (*Photo by courtesy U. S. Forest Service.*)

The most successful shade plants are the dwarf or creeping shrubs, such as *Gaultheria procumbens, Vaccinium oxycoccus, Cornus canadensis, Mitchella repens,* and *Epigæa repens,* with which are associated *Coptis trifolia, Clintonia borealis, Pyrola elliptica, Chiogenes hispidula, Aralia nudicaulis,* etc. The various species of *Sphagnum* usually disappear before the subclimax is reached, but *Polytrichum* and *Cladonia* sometimes persist into the climax.

The Spruce-Pine Forest.—This association covers northern British Columbia, the Yukon, and Alaska up to the limits of the tundra in the north and to an altitude of 1,000 to 2,000 feet in the mountains. It possesses the white spruce in common with the eastern association, but the balsam fir and jack pine have disappeared, the larch is rare in Alaska, and the black spruce much less frequent. The three deciduous species,

especially the paper birch, play a much larger part, and two new dominants enter from the subalpine forest of the Rocky Mountains, namely, lodgepole pine, *Pinus contorta murrayana*, and alpine fir, *Abies lasiocarpa*. In the north, even the white spruce becomes subordinated to the poplars and birches, though it persists in the south to Cook Inlet and beyond, where it is mixed with *Picea sitchensis*, *Thuja plicata*, and *Tsuga mertensiana* of the coast forest. Owing to the fact that the peninsula of Alaska is largely surrounded by cold waters, and as well to the number of mountain ranges, its climate is Arctic and tundra is the prevailing climax. It is chiefly along the Yukon River and its tributaries, and the Pacific Ocean, that forest climaxes are possible.

The bogs of black spruce and occasional larch exhibit many of the heaths and other shrubs of the eastern association, and the undergrowth of the climax areas is likewise much the same, until the influence of the Pacific Ocean is felt. In such regions, *Alnus*, *Cornus*, *Ledum*, *Ribes*, *Vaccinium*, and *Viburnum* are joined by *Gaultheria shallon*, *Menziesia*, *Echinopanax*, etc., from the coast forest, and this undergrowth becomes controlling in mixtures of the two climaxes.

The Birch-Aspen Associes.—This is the characteristic fire subclimax throughout both associations. It is composed chiefly of the paper birch and aspen, though the balsam poplar and jack pine take some part in it. The first two may appear as pure or nearly pure consocies, or they may be mixed in various degrees, often with a sprinkling of balsam poplar. The latter is rarely pure, except occasionally on flood plains, but the jack pine usually constitutes a consocies, owing to the relation between its closed cones and seeding. Birch and aspen occur more or less abundantly as relicts in the climax forest, and particularly at the margins, where fire and clearing have been at work. They are, however, at an increasing disadvantage in competition with the climax dominants as the latter grow taller, and they gradually drop out and finally disappear in the mature forest. The undergrowth is better developed than in the climax as a result of the more open canopy. It is often dominated by *Pteris aquilina*, which finally yields to the original forbs of the climax.*

The Subalpine Forest

Extent and Nature.—As has been indicated earlier, the three great mountain systems of the continent have served as pathways for the

* The student may well consult the following general sources of information on plant communities of North America:

Shantz and Zon, "Natural Vegetation"

Clements, "Climax Formations of Western North America," in *Plant Indicators*. "Naturalist's Guide to the Americas."

Harshberger, "Phytogeographic Survey of North America."

southward extension of the boreal forest during cold-wet phases of the climatic cycle and as refuges for it with the return of warm-dry phases. Because of its lower elevation, the Appalachian system has been less effective in this respect; but one or two new species have been evolved and the subalpine community is poorly developed and little differentiated from the boreal. It has been quite otherwise on the much higher ranges of the Rocky Mountains and the Sierra-Cascade system. Not only are all the conifers different in species from those of the boreal forest proper, but they also differ decisively in the two associations of the subalpine forest. The deciduous trees have, moreover, decreased both in number and abundance, the three major species now being represented only by the aspen, except for the northern portions of the Rocky Mountains.

As the name suggests, the subalpine forest occupies the upper slopes of the high ranges, usually forming a belt 2,000 to 3,000 feet in altitude between the alpine tundra above and the montane climax below. It stretches from southern Alaska and adjacent British Columbia to Mexico and Lower California, wherever the altitude is sufficiently great. It is found on all the higher ranges of the Great Basin but in reduced form and reaches its eastern limit on the Front Ranges of the Rockies from New Mexico northward.

The subalpine climax bears a relationship to three different formations, namely, the boreal, the coast, and the montane forest. The direct relationship is with the first, since the chief dominants of both belong to the two genera *Picea* and *Abies*, the species of which are also related. The general connection with the coast forest is shown by the presence of *Abies*, *Larix*, and *Tsuga* in both, though represented by different species. *Picea engelmanni*, moreover, is fairly common and *Abies lasiocarpa* not infrequent in the transition association. The relationship to the montane forest is indicated by the presence in each of closely related species of *Picea* and *Abies*, though these two genera play a less important rôle in the lower zone. *Pinus contorta* and *Populus tremuloides* are common to both, though much more abundant in the subalpine region (Figs. 34 and 95).

In spite of its occurrence on many separate ranges, the subalpine forest possesses a high degree of unity. Its two chief dominants, *Picea engelmanni* and *Abies lasiocarpa*, occur practically throughout, except for California. *Pinus contorta* extends from the mountains of Yukon to the San Pedro Martir of Lower California and the Front Ranges of Colorado. *Pinus flexilis* and *P. aristata* are found through the larger part of the two associations, though represented by distinct varieties. Two other important dominants are *Tsuga mertensiana* and *Larix lyallii*, which, though essentially coastal in character, occur in the transition area of northern Idaho and Montana, *Larix* even reaching the Rockies in southern Alberta. The other important dominant, *Abies magnifica*,

though found only in California and southern Oregon, may well be regarded as the ecological representative of *A. lasiocarpa.*

The ecological unity of the subalpine formation is emphasized by its constant relation to the montane forest below and the alpine tundra above it. Its geographic and topographic relations serve to explain the uniformly boreal climate in which it flourishes. This is characterized by a short growing season, relatively high precipitation, mostly in the form of snow, and wide diurnal and seasonal range of temperatures. The long winter is marked by high winds and excessive transpiration in relation to the holard, and these have a controlling influence in determining the holard.

The two associations reflect the wide separation of the two Cordilleras, except in the north, and the resulting differentiation of two subclimates. The warrant for distinguishing them is found in the fact that *Picea engelmanni* and *Abies lasiocarpa* are the two major dominants in the Rocky Mountains but are lacking in California; that *Tsuga mertensiana* and *Abies magnifica* are confined to the western association; and that the two pines, though closely related, are represented by different varieties or nascent species. *Pinus contorta,* moreover, assumes the rôle of a climax dominant in the Sierran community, while its variety *murrayana* is a subclimax one in the Petran.

Petran Subalpine Forest.—This association extends from the mountains of northern British Columbia and Alberta to northern New Mexico and Arizona. It also occurs on the Blue Mountains of Washington and Oregon and in reduced form is found on the higher ranges of the Great Basin and southward along the Sierra Madre into Mexico. In altitude, it ranges from 3,000 to 7,000 feet in the north and from 8,000 to 12,000 feet in Colorado and New Mexico.

The precipitation in the central part of the area varies from 22 to 40 inches a year, and the snowfall from 8 to 14 feet. On the interior ranges the rainfall may be somewhat less. The evaporation is lower than in the montane zone, the reduction ranging from 25 to 50 per cent. At the lower limit, the growing season is nearly 4 months long; at the upper, between 2 and 3 months. The mean temperatures are 5 to 10 degrees less than in the montane forest, and near timber line frost occurs frequently during the summer.

The mass of the association is constituted by *Picea engelmanni* and *Abies lasiocarpa,* much fragmented in the north by the burn communities of *Pinus contorta murrayana*[38] (Fig. 247). *Pinus flexilis* and its variety *albicaulis* are more abundant northward and even *Larix lyallii* enters the community in southern Alberta. In northern Colorado the usual grouping is *Picea, Abies, Pinus murrayana* and *P. flexilis,* while southward the lodgepole pine drops out and *Pinus aristata* appears. On the desert ranges of the interior, *Pinus flexilis* and *aristata* alone remain to

represent this climax. The characteristic fire subclimax is formed by the lodgepole pine, *Pinus murrayana*, which covers great areas with a pure stand from central Colorado northward. It is often accompanied by aspen, which finally yields to it, while beyond the range of the pine, the former constitutes similar subclimaxes. Mixed societies of grasses and forbs usually attain a striking development in the aspen community, but they are much reduced under the denser canopy of the pine or of the spruce-fir climax. The most important genera are *Aquilegia*, *Arnica*, *Campanula*, *Castilleja*, *Erigeron*, *Fragaria*, *Polemonium*, *Solidago*, and *Thalictrum*, many of them represented by the same or related species in the montane forest.[22,382,383]

FIG. 247.—Petran subalpine climax of Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*), in Colorado.

Sierran Subalpine Forest.—Certain dominants of this association reach their northern limit in Alaska, but in its more typical expression this forest stretches southward from British Columbia along the upper slopes of the ranges. Its eastern limits are found where it comes in contact with the Petran association in Alberta and Montana or on the eastern slopes of the Sierra Nevada. It is much reduced in the cross-ranges of southern California and its last outposts disappear in Lower California. The altitude of this zone rises steadily from Alaska southward, from 2,000 to 4,000 feet at the north, 5,000 to 8,000 feet in the central portion, to 7,000 to 10,000 feet in the Sierra Nevada. The climatic relations are much the same as in the Petran association, with the important exception that the precipitation is much higher, ranging

in the Sierras from 50 to 75 inches. A half to nearly all of this may fall as snow, the total snowfall sometimes exceeding 50 feet in depth.

The characteristic dominants of this forest are six, namely, *Tsuga mertensiana*, *Pinus contorta*, *P. flexilis albicaulis*, *P. aristata balfouriana*, *Larix lyallii*, and *Abies magnifica*. Three other dominants, *Picea engelmanni*, *Abies lasiocarpa*, and *Pinus flexilis*, are more typical of the Petran forest, while *Abies amabilis*, *A. nobilis*, *Pinus monticola*, and *Chamæcyparis* are more important in the coast forest. The two dominants of

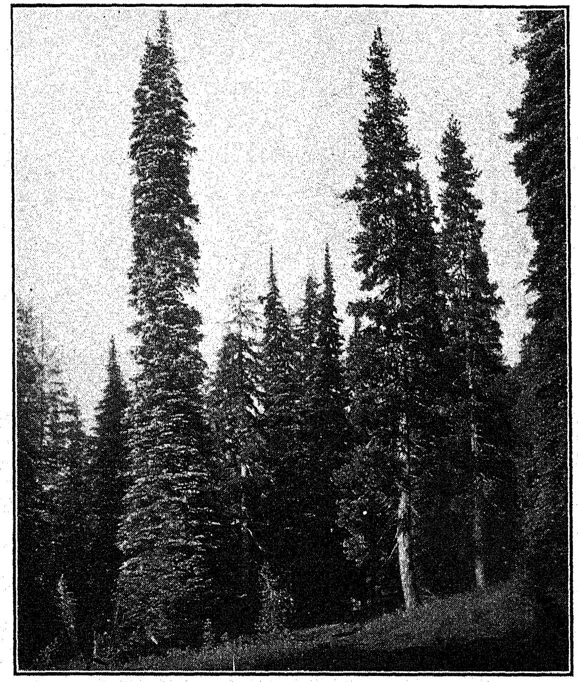

FIG. 248.—Sierran subalpine climax of subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*), in Oregon.

the greatest extension are *Tsuga* and *Pinus contorta*, ranging from Alaska to the southern Sierras, while *P. albicaulis* occurs from British Columbia to the thirty-sixth parallel. *Larix* is more restricted, while *Abies magnifica* is confined to California and Oregon, and *Pinus balfouriana* grows only in California (Fig. 248).

The large number of dominants and the extensive range make the groupings exceedingly varied. There is a marked tendency toward pure consociations near timber line, while in the lower part of the zone two or more dominants usually occur in mixture. In the ranges of the upper Columbia Basin, *Abies lasiocarpa* and *Picea engelmanni* are regularly present and are usually associated with one or more of the following:

Pinus contorta, *P. albicaulis*, *Larix*, and *Tsuga*. *Tsuga* and *Abies* are found together in Alaska, while farther south *Picea*, *Larix*, *P. albicaulis*, and *Abies amabilis* are commonly associated with them. In the Sierra Nevada, *Tsuga* occurs with *Abies magnifica*, *Pinus contorta*, and *P. monticola* through most of the width of the zone and with *P. albicaulis* in the upper portion. *Pinus balfouriana* is associated with the first group in the lower portion of the forest, with *P. monticola* higher up and with *P. albicaulis* at timber line.

The Sierran subalpine forest is not rich in societies and most of those present have been derived from the alpine tundra or the montane forest, the shrubs, in particular, coming from the latter.

The Lake Forest

Extent and Nature.—As the name implies, this is preeminently a lake formation, being centered on the Great Lakes and recurring to the eastward in New York and New England where the larger lakes and rivers produced similar conditions. Since sandy soils likewise furnish favorable water and temperature relations, the pines, in particular, are to be found on sandy plains through much of this region. The most extensive stands of white pine, *Pinus strobus*, were originally found in central and northern Michigan and in eastern central and northern Minnesota. Farther east, the forest was more fragmentary, consisting chiefly of relict communities of varying size, found about bodies of water, on sandplains, or on the slopes of the Allegheny Mountains in Pennsylvania and to the southward. The climax dominants, white and red pine and hemlock, occur over a much wider area, smaller relicts, as a rule, persisting through southern Ontario and Quebec, much of New Brunswick and central Maine.

The climate of this forest has a wide geographic as well as annual range. The annual precipitation varies from a mean of 25 inches in Minnesota to one of nearly 45 inches in the mountains of the East. The temperature extremes during the year may range from $-50°$ to 105°F., and in the northern portion frost may occur in any month of the summer. The growing season averages 4 months, though white pine and hemlock persist under favorable local conditions in regions where it is much longer.

The Pine-Hemlock Forest.—The lake forest consists of a single association, in which *Pinus strobus*, *P. resinosa*, and *Tsuga canadensis* are the climax dominants. It has been so long cut off from the related montane and coast forests of the West that they can not be grouped in the same climax, though their phylogenetic relationship seems evident. In fact, the climax nature of the lake forest itself may be easily questioned today, because of the great vicissitudes it has experienced. No other association has suffered so severely from lumbering and consequent fire, partly

because of the quality of its timber, but chiefly because of its proximity to long-settled and well-populated districts. In southern Ontario where white pine with considerable red pine constituted formerly 60 per cent of the forest, logging and fire have reduced this to scattered relicts, about which effective reproduction is still further handicapped by the coactions of man. It is such universal disturbance that is primarily responsible for the doubts as to the actual existence of a pine-hemlock climax, but earlier historical and physical factors have had a large share as well.

During the repeated mass migrations of the glacial-interglacial cycles, this entire climax suffered not only the most severe buffeting but also the most intense competition from the boreal forest along one border and the deciduous forest on the other. Its migration before the ice front or in the wake of its retreat was, moreover, peculiarly handicapped by the solidarity of the great mass of the hardwood forest and, during the Recent period, by that of the boreal forest as well, to say nothing of the barriers constituted by the Great Lakes. In a region with such marked extremes of climate, each phase of every major climatic cycle has increased its disadvantage. The cold-wet phases have permitted the encroachment of the boreal climax, the warm-dry ones that of deciduous forest, not over a uniform terrain but one fragmented by lakes, rivers, and mountain ranges to the extreme. One striking consequence has been the inclusion of many small, relict areas of pine, hemlock, or both well within the mass of deciduous or boreal forest. When all the evidence is assembled and weighed in the light of these various processes, there seems little doubt that the pine-hemlock forest represents a genuine climax, now sadly depleted and fragmented, especially by the hand of man.

The climax dominants of this association are red or Norway pine, *Pinus resinosa*, white pine, *P. strobus*, and hemlock, *Tsuga canadensis*. A frequent associate of the pines is the jack pine, *P. banksiana*, but this belongs properly to the subclimax. On mountain slopes the red spruce, *Picea rubra*, is associated with white pine especially but is, perhaps, even more frequent in montane communities of white spruce and balsam fir. To the southward, *P. rigida* also enters this community and serves to connect it with the subclimax pine forest of the southeast. The arborvitæ, *Thuja occidentalis*, often plays a rôle of considerable importance, but it, too, is to be regarded as a subclimax species. The white cedar, *Chamæcyparis thyoides*, likewise exhibits affinities with this group but is rarely of much importance even in the subclimax (Fig. 249).

The difference in the ecological requirements of the three climax dominants is such that they are not frequent in mixture, but this has undoubtedly been, in part, an outcome of lumbering. The two pines occur together throughout most of the western portion, but the greater

tolerance of the white pine for shade originally produced extensive pure stands.[30,110] Over the eastern part of the area, the relict areas appear, as a rule, to be either pure pine or hemlock, but in the original forest the two consociations grew side by side as well as in mixture.[47,367] The view that hemlock is properly a member of the deciduous forest runs counter to the rule as to the identity of life-forms and has not taken sufficient account of the nature of relicts. Since its tolerance of shade and its water requirements are greater than those of the white pine, the

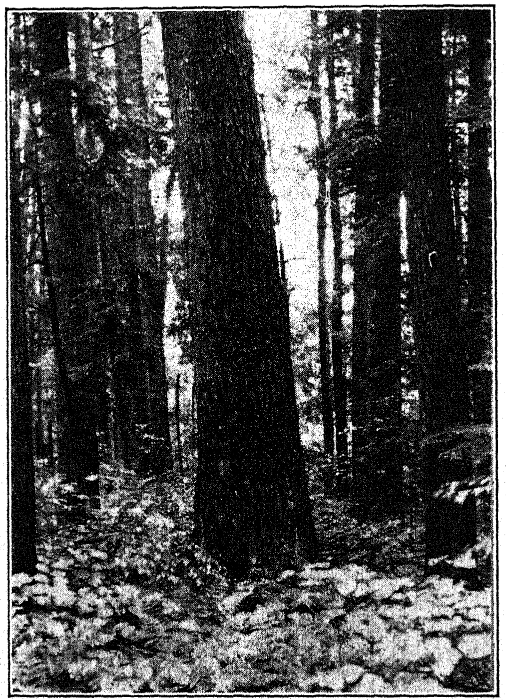

FIG. 249.—Pine-hemlock forest (*Tsuga canadensis* and *Pinus strobus*) in Pennsylvania. (*Photo by courtesy of U. S. Forest Service.*)

hemlock approaches beech, maple, and chestnut closely in its demands. Its proper climax position is disclosed, however, by the relict communities in the maple-beech association, where it is found all but invariably on the cool-moist northerly slopes.[581]

The number of genera common to the pine-hemlock association and the coast and montane forest of the West is so great as to indicate that they were originally derived from the same coniferous climax. The transition association of the coast climax, in particular, has a species corresponding to practically every one of the lake forest. *Pinus strobus* is represented by another white pine, *P. monticola;* the red pine by the yellow pine, *P. ponderosa;* and the jack pine by another species of the

same character, *P. contorta.* *Tsuga canadensis* has a reciprocal species in *T. heterophylla*, *Thuja occidentalis* in *T. plicata*, and *Larix laricina* in *L. occidentalis*. The presence of *Chamæcyparis* on both coasts is a further point of resemblance. The montane forest is more nearly related to the coast climax, but it also contains the three types of pine as well as a group of more recently evolved southern pines corresponding, in some measure, to the numerous species of the pine subclimax of the Southeast.

The characteristic subclimax of the pine-hemlock forest is formed by the consocies of jack pine, *Pinus banksiana*. As in practically all species of this group, the cones not only remain on the trees for a number of years, but also they open tardily and sometimes only as a result of fire. This species is, in consequence, especially fitted to take possession of burned areas as pure stands; its preference for sandy plains is likewise to be explained by its lower requirements, though in such situations it may be the subfinal stage of the normal prisere. Birch and aspen also occur in a fire subclimax in this forest, though largely as a result of mixture with the boreal formation. *Thuja occidentalis* is regarded as the typical subclimax of the hydrosere, usually forming a fairly distinct and nearly pure zone about the drier margins of bogs. At its inner edge it is frequently associated with *Picea mariana* and *Larix laricina;* though the latter belong properly to the boreal climax, the frequent occurrence of relict bogs in the northern portions especially of the pine-hemlock climax gives these two species more or less subclimax importance in the latter.

The undergrowth of this forest is rather poorly developed, owing to the dense canopy, particularly in the hemlock consociation. Moreover, from its position, the species of shrubs and herbs are common to boreal or deciduous forest for the most part. They are necessarily shade plants of a more or less extreme type, largely ferns and fernworts, *Asplenium, Polystichum, Lycopodium;* orchids, *Calypso, Goodyera;* saprophytes, *Corallorrhiza, Monotropa, Hypopitys;* and such undershrubs and forbs of the ground cover as *Mitchella, Chimaphila, Gaultheria, Pyrola, Circæa, Viola,* etc.

The Coast Forest

Extent and Nature.—This climax has its greatest development along the Pacific Coast, as its name implies. The main body stretches from southern British Columbia to northern California, but several of the major dominants extend much farther northward as well as southward. *Picea sitchensis* finds its northernmost limit at Cook Inlet in Alaska, while *Tsuga heterophylla* and *Chamæcyparis nootkatensis* reach nearly as far. *Thuja plicata* occurs in southern Alaska, and *Abies amabilis* is found at the extreme southern end. *Sequoia sempervirens* ranges farthest to the south, its last outposts lingering in the Santa Cruz and Santa

Lucia Mountains of California. While the best expression of this climax is along the coast, it extends to the Cascades and covers their western slopes. Eastward it passes into a broad transition forest that reaches to the western ranges of the Rocky Mountains in northern Montana and adjacent British Columbia. In altitude, the coast forest extends from sea level to 3,000 to 5,000 feet in the coast ranges and the Cascades.

Geographically, this forest belongs to the coast and the Columbia Basin. At the higher levels, the latter resembles the former in being a region of relatively high rainfall and low evaporation. The exceptional extension along the coast is partly a matter of high rainfall but is due chiefly to the remarkable oceanic compensation between Alaska and California. The temperatures as well as the rainfall are less uniform from east to west, but this is reflected in the mixing of two climaxes and the differentiation of a transition community.

The closest relationship of the coast forest is with the montane climax, due, in some degree, to their direct contact at present. This is naturally best exemplified in the transition association, while the generic composition of the coast association is more like that of the pine-hemlock forest of the Northeast, as already indicated. Both the former show an affinity with the boreal forest in the presence of *Abies* and *Picea,* though this may really be through the subalpine forest. The most important dominant in common is the Douglas fir, *Pseudotsuga mucronata,* which reflects the climatic relations in being climax in the montane formation and subclimax in the higher rainfall of the Northwest. The chief contact of the coast forest is with the montane, until this yields in the north to the subalpine and the latter to the western association of the boreal climax. About Cook Inlet the grouping may include a single dominant of each of the last three.

The Cedar-Hemlock Forest.—This is much the more massive and continuous of the two associations. The dominants are fewer and the composition less varied, though the northern and southern extremes show striking differences from the central portion. The trees are taller, the canopy denser, and the shrubby layer often developed to form almost impenetrable thickets. The most typical expression is found in western Washington and British Columbia, whence the forest decreases in width and number of dominants in both directions, *Picea* and *Tsuga* forming the northern and *Sequoia* the southern outposts.[362,393]

The essential character of the coast forest is given by *Tsuga heterophylla, Thuja plicata, Picea sitchensis,* and *Sequoia sempervirens,* though the typical grouping comprises the first two together with *Pseudotsuga mucronata. Picea* is confined to the vicinity of the seacoast and *Sequoia,* though more southern, restricted chiefly to the fog belt; the several species of *Abies* and *Chamæcyparis* range well into the adjacent communities.[111] With respect to abundance and extent, *Pseudotsuga* is much the most

important dominant. It is the typical species of burned areas and, hence, properly constitutes a subclimax, a conclusion further supported by its relatively low tolerance.[245] Much of the area formerly covered with *Tsuga*, *Thuja*, and various associates is now a pure stand of Douglas fir, in which the hemlock and cedar persist in deep canyons or other protected places. This species is likewise a major dominant of the montane forest as well as of the transition association and, in consequence, passes readily from the rôle of subclimax to climax dominant.

This association constitutes a coniferous forest of unrivaled magnificence, in which the mature trees reach heights of 200 to 300 feet and diameters of 15 to 20 feet.[363] This is a direct outcome of the moderate

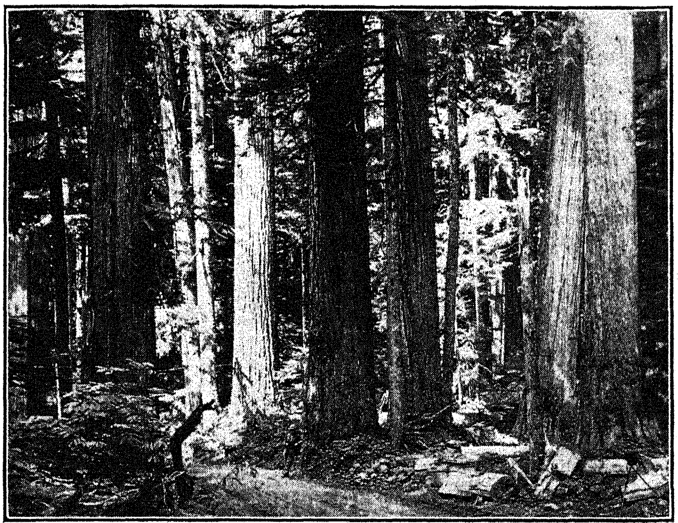

FIG. 250.—Climax forest of western hemlock (*Tsuga heterophylla*), white cedar (*Thuja occidentalis*), and Douglas fir (*Pseudotsuga mucronata*), Mount Rainier, Washington.

temperatures and excessive rainfall with frequent or constant fog. Over much of the area the annual rainfall is in excess of 80 inches, the range being 50 to 120 inches. In the United States, all but 10 to 30 per cent of this falls during the 6 winter months, and much the same conditions obtain to Sitka and beyond. The absolute minimum as far north as Sitka is but −4°F. (Fig. 250).

In a region of such excessive precipitation, the water relations of the dominants are less clear or at least are much modified by temperature. The general relation to the factor complex is indicated by the altitudinal range, though this is not in full accord with that of latitude. The typical fog-belt trees are *Picea sitchensis*, *Sequoia sempervirens*, and *Chamæcyparis lawsoniana*, which indicate maximum conditions as to water content and humidity. These are followed by *Thuja plicata* and this by *Tsuga*

heterophylla and *Abies grandis*. The ability of *Abies amabilis*, *A. nobilis*, and *Chamæcyparis nootkatensis* to endure more xeric conditions is shown by the fact that they occur also in the subalpine zone, where the first is frequent at timber line. *Pseudotsuga* is the most xeroid of all the dominants, a fact in complete accord with its subclimax nature and its importance in the montane forest.

Shrubby societies are characteristic of this forest and those of forbs are correspondingly reduced. *Gaultheria shallon* and *Echinopanax horridum* are two of the most typical subdominants, while *Acer*, *Berberis*, *Ribes*, *Rubus*, *Rhododendron*, *Sambucus*, and *Vaccinium* are the genera represented by two or more species. Among the ferns, *Blechnum spicant*, *Polystichum munitum*, and *Pteris aquilina* are widespread, while the ground cover is composed chiefly of *Oxalis oregana*, *Asarum caudatum*, *Fragaria vesca*, *Trientalis latifolia*, *Trillium ovatum*, *Disporum smithii*, *Streptopus rosea*, etc.

The Larch-Pine Forest.—This association occupies the eastern slopes of the Cascades below the subalpine zone. It stretches across the mountains of northern Washington into Idaho and northwestern Montana, reaching its limit on the western slopes of the Continental Divide. It is found on the Gold and Selkirk ranges of British Columbia, the southern Bitterroot Mountains of Idaho, and the Blue and Wallowa ranges to the west.[559]

This is primarily a transition forest between the coast and the montane climaxes, but it occupies such a large area that it can not well be regarded merely as an ecotone. Over most of the region the dominants of the coast forest are characteristic, and for this reason it is assigned to this climax. The trees, however, are reduced in size and the association is less dense and exclusive, owing to increasing remoteness from the coast. Of the four major dominants of the coast association, *Picea sitchensis* has disappeared, *Tsuga* and *Thuja* diminish in importance and then disappear, and *Pseudotsuga* shares the control with several other important species. Over most of this forest the rainfall is only 20 to 35 inches, and 30 to 60 per cent of this falls between the first of April and the end of September, a proportion twice as great as in the cedar-hemlock forest. The mean temperature is about 7° lower and the minimum ranges from $-25°$ to $-49°$ (Figs. 96 and 173).

The chief contact of the transition forest is with the montane climax, and, in consequence, its dominants are almost equally divided between the two formations. Five are derived from the coastal association and three from the montane forest, while *Pseudotsuga* belongs to all three but is here more of the montane type. *Pinus monticola* and *Larix occidentalis* reach their optimum development in northern Idaho and the adjacent regions and may well be regarded as the two most typical dominants of this forest. Likewise, while *Abies grandis* ranges from the coast to north-

western Wyoming, it is more characteristic of the transition region. Toward the east the major dominants of the coast association are the first to drop out, followed by those of the transition community, while *Pseudotsuga*, *Pinus ponderosa* and *contorta*, and *Picea engelmanni* continue into the Rocky Mountains as chief dominants. The undergrowth varies in harmony with the behavior of the dominants; it is essentially the same as in the cedar-hemlock forest in the western portion, becomes a mixture in the central, and finally passes over more or less completely into that of the montane forest in the east.

The Montane Forest

Extent and Nature.—This is the most extensive and, perhaps, the most important of all the western forest climaxes. It extends from the foothills of western Nebraska and South Dakota and the mountains of western Texas to the Pacific Coast and reaches from the mountains of central British Columbia to those of Mexico and Lower California. It occurs throughout the ranges of the Great Basin and on those of the southwestern deserts where the altitude permits. Geographically, this formation is typical of the great Cordilleran system, from which it extends out upon the many plateaus to the eastward as well as in the interior. Its climatic range rivals that of the grassland in so far as latitude is concerned, both extending several degrees northward into Canada and even farther southward into Mexico. The vertical range of this climax is often more than 6,000 feet in the Rocky Mountains and it may be somewhat more in the Sierras and Cascades. The corresponding range in rainfall and temperature is vast. The pine consociation of this forest frequently occurs in a rainfall of 20 inches or less from Colorado to Arizona and in one of 50 to 60 inches on the Pacific Coast. As to distribution, 50 per cent or more falls in summer along the Rockies, while along the Sierras and Cascades 70 to 90 per cent falls during the winter. As to temperature, there is a difference of more than 20° in the mean for northern Montana and southern California and of 60° in the lowest recorded minimum. In spite of this, the regular association of the three major dominants throughout the area indicates that the climate is essentially a unit from the standpoint of vegetation.

In structure, the montane forest is most closely related to the coast climax, as is shown by the broad transition between the two and by the importance of *Pseudotsuga* in the two. Its widest contact is with the subalpine formation, the two touching and mingling for thousands of miles along the ranges of the Rocky Mountains and the Sierra-Cascade system. These two forests are similar in appearance, but they differ fundamentally in composition, origin, and climatic and successional relations. Along the lower margin, the montane forest makes the most

varied contacts, touching woodland in the south, grassland along the eastern front, chaparral in California especially, and this or sagebrush in the ranges of the Great Basin.

The unity of this vast formation is demonstrated by the occurrence of the three major dominants, *Pinus ponderosa*, *Pseudotsuga mucronata*, and *Abies concolor*, from Colorado to California and from Montana to Mexico. It is further emphasized by the more or less constant presence of *Pinus contorta*, *P. flexilis*, and *P. albicaulis* in both associations. There is also marked agreement as to the genera of the societies, more than three-fourths of these being common to both.

The Petran Montane Forest.—This is the characteristic forest of all the ranges between the Great Plains and the Sierra-Cascade axis and is by far the most extensive of all the forest associations of the continent. At the north its area is relatively narrow where it yields to the coast forest in Montana and British Columbia, and it is broadest in the center, where it stretches from western Nebraska to the eastern slopes of the Sierras in Nevada. The range in altitude naturally varies with the latitude; in general, it is from 4,000 to 7,000 feet in the north to 6,000 to 9,000 feet in the south, but the consociation of *Pinus ponderosa* in the form of savannah often extends much lower.

By virtue of their abundance and wide occurrence, *Pinus ponderosa*, *Pseudotsuga mucronata*, and *Abies concolor* take rank as the major dominants of this association.[384] The lodgepole pine, *P. contorta murrayana*, comes next; it is typically the subclimax dominant of the burn subsere but is so exclusive and permanent owing to repeated fires that it is conveniently considered along with the climax. *Pinus flexilis* and its variety *albicaulis* are of wide range both in altitude and in geographical area but generally of secondary abundance. Several other pines are of local importance in Arizona, New Mexico, and Mexico, but these are all of restricted distribution, as is also the one spruce, *Picea pungens*, in the central Rockies. In general, *Pinus ponderosa*, *Pseudotsuga*, and *Abies* occur together throughout the mass of the association. To the northwest, *Abies* becomes secondary or is absent, while in the Wasatch Mountains of Utah the pine is usually lacking and in the desert ranges the Douglas fir. The lodgepole pine covers large areas in the central and northern Rockies but disappears to the southward, where its subclimax rôle in burns is taken by the aspen[285,582] (Fig. 251).

The most xeroid of the major dominants is *Pinus ponderosa*, followed by *Pseudotsuga* and *Abies;* the most mesophytic is *Picea pungens*. *Pinus c. murrayana* is nearly as xeric as the yellow pine, but has a wider range of adaptation. Much the same is true for *P. flexilis* and *albicaulis*, while the three southern pines resemble *P. ponderosa* in this respect. The rainfall limits for the montane forest are approximately 18 to 20 inches for the lower margin and 22 to 23 inches for the upper, though the yellow

pine persists in savannah with a precipitation of 15 inches and lodgepole outposts may be found at even lower limits (Fig. 30).

The shrubby layers of the montane forest are fairly well developed, the genera, for the most part, being much the same as in the deciduous and pine forests of the East. The lower layer consists of *Opulaster*, *Rosa*, *Viburnum*, *Ribes*, *Jamesia*, etc., and the more open upper one of *Acer glabrum*, *Betula occidentalis*, *Prunus pennsylvanica*, *Cornus amomum*, etc., together with scattered aspens and willows. The herbaceous societies are also grouped in two layers and exhibit two well marked

FIG. 251.—Yellow pine (*Pinus ponderosa*) consociation of the montane forest.

aspects, spring and summer, with the autumn one brief and less distinct. The characteristic genera of the upper layer are *Mertensia*, *Thalictrum*, *Geranium*, *Actæa*, *Castilleja*, *Erigeron*, *Solidago*, *Aquilegia*, and *Haplopappus*, while the ground carpet is composed of *Fragaria*, *Viola*, *Pyrola*, *Atragene*, *Saxifraga*, *Goodyera*, etc.

The Sierran Montane Forest.—This forest extends to central Oregon along the Cascades but little beyond the border in the Coast and Siskiyou ranges. In its typical expression it is practically confined to California, where it is replaced by the coast forest in the northwest and by the Petran along the eastern slope of the Sierra Nevada. It is fragmentary in the southern Coast ranges but is the characteristic forest of the Cross Ranges, reaching its southern limit in reduced form in the mountains of Lower California. The range in altitude is exceptionally great; in the north it occurs at 1,000 to 3,000 feet in the Coast ranges and at 2,000 to

6,000 feet in the Cascades. In the central Sierras the limits are much the same, but the upper limit rises to 7,000 to 8,000 feet in southern California and even to 8,000 to 10,000 in Lower California.

The major dominants of the association are *Pinus lambertiana*, *P. ponderosa*, *Pseudotsuga mucronata*, *Abies concolor*, and *Libocedrus decurrens*. All of these occur from the northern limit in Oregon to the San Pedro Martir Mountains of Lower California, though the Douglas fir is represented in the south by the variety *macrocarpa*, as the yellow pine is at the upper limits by its variety *jeffreyi*. The remaining species are all of secondary importance, three of the pines, *P. attenuata*, *muricata*, and *radiata*, taking the rôle of a fire subclimax in the various areas, after the model of the lodgepole pine in the related association. Of frequent occurrence are three species of broad-leaved trees, *viz. Quercus californica*, *Q. garryana*, and *Arbutus menziesii*, the latter an evergreen suggestive of the rôle of *Magnolia* in the East. These are considered to be relicts of former more extensive forests of similar type and now play a subclimax part, especially in the fire succession (Fig. 252).

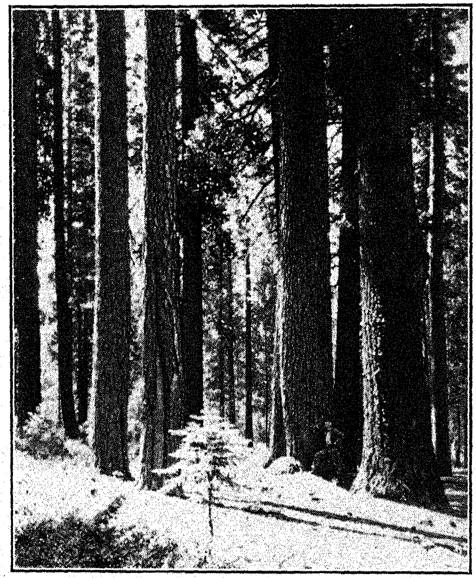

Fig. 252.—Sierran montane forest of yellow pine, sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*), Yosemite, Calif.

This association grows under a rainfall of 80 inches in the coast ranges of northern California, but this amount decreases rapidly toward the south until it reaches 20 inches in the San Jacinto and San Pedro Martir Mountains. In spite of this, the great mass of the association is constituted by the five major dominants, though in the most variable proportions.

While mixed forest is the rule, yellow pine and Douglas fir often occur in extensive pure stands, or they may be mixed more or less equally. *Abies concolor* may occur pure, but to a lesser degree, while *Pinus lambertiana* and *Libocedrus* are practically always found in mixture, of which they rarely make more than 15 per cent. *Sequoia gigantea,* which is localized in the central Sierras, is occasionally found in pure communities but is usually associated with *P. lambertiana* and *Abies.*

The most important subclimax tree is *Pinus attenuata,* which ranges throughout the Sierras as a dominant in burns. In general, however, fire-swept areas are covered for a long time by a subclimax chaparral very like that of the foothills in ecological behavior but composed, for the most part, of different species of the same genera, *Ceanothus, Arctostaphylos, Quercus, Prunus, Rhamnus,* etc. With the return of the forest, these persist in decreasing number and abundance as a shrubby layer until the dense canopy of the climax precludes the great majority of them. As the shrubs decrease, the herbaceous layers become more important and remain characteristic of all but the densest climax portions. The genera are largely the same as in the Petran association, a small number such as *Adenocaulon, Microseris, Monardella,* and *Lotus* being restricted wholly or chiefly to the Sierran region.

THE DECIDUOUS FOREST

Extent and Nature.—This is unique in being the only formation of the deciduous life-form on the North American continent, though there are relicts of related communities on the Pacific Coast and in Mexico. It is directly related to the similar forest of central Europe and Asia, the generic dominants being practically the same but the species almost wholly different. It is essentially a temperate forest, in contrast with the coniferous forests of the boreal and mountain regions, on one hand, and the evergreen tropical forest, on the other. Together with the grassland it makes up the great vegetation mass of the continent, and their broad contact and reciprocal movement render it desirable to treat them in sequence, in spite of the difference in life-form. The striking feature of this relation is the great wedge that has been driven into the forest by climatic changes, the apex of which lies in western Indiana, while outposts of the movement are still to be found in Ohio and Michigan.

The general northern limit of the deciduous forest runs from central Minnesota along the southern shore of Lake Superior eastward to southwestern Quebec. Throughout much of Nova Scotia and New Brunswick, except the colder coastal regions, it alternates or mixes with the boreal forest, and it bears a somewhat similar relation to this and the pine-hemlock forest along the northern shores of Lake Huron and Lake Superior to its northwestern edge in Manitoba. From southern Maine

it stretches south to central Georgia, southern Louisiana, and eastern Texas. Relicts of it occur throughout the coastal plain and as far south as the Everglades and indicate that the pine forests of this region are to be regarded as subclimax. On the west, a fairly continuous body of hardwoods extended from northeastern Texas and adjacent Oklahoma through the southern half of Missouri and lower Illinois to Indiana and thence northwest through southern Wisconsin to southeastern Minnesota. Long tongues of the oak-hickory association persist along all streams of the subclimax prairie and in reduced form along the rivers of most of the true prairie. Two large bodies of xeric species of oak occur in Texas and Oklahoma, where they are known as Cross Timbers and constitute relicts of a former much wider extension of this formation.[526]

As already suggested, the deciduous forest has no phylogenetic relationship with any other existing climax of North America, its nearest relatives being the similar forests of Eurasia, from which it has long been separated. The evidence from paleo-ecology, however, shows that many of its dominants once stretched much farther west and indicates that the oak communities of the Pacific slope are remnants of such early forests. The longest and most significant contact of the hardwood forest is with the prairie, the two alternating over a large portion of the Middle West. On the north the interruption caused by the Great Lakes has served to obscure the contacts with the coniferous climaxes and the three climaxes mix and alternate with each other to almost every conceivable degree. The climatic limit on the south and east is probably the Atlantic Ocean and the Gulf of Mexico, but the actual contact is with a broad belt of pines mixed with hardwoods, with which the relation is that of climax and subclimax.

As in other vast formations, the climatic relations exhibit a wide range, the rainfall from east to west and the temperature from north to south. The maximum precipitation occurs in the south and east, where it reaches 50 to 60 inches; the minimum is found in the northwest with less than 30 inches, owing to the compensating action of decreased evaporation. For the same reason, the western margin of the hardwood climate runs from somewhat more than 35 inches in Texas to about 25 inches in Minnesota. The growing season in the northern portion is about 5 months with an average temperature of about 60°F., while for the southern part it is 2 or 3 months longer and the average about 65°F.

The unity of the climax is shown by the large number of major dominants that occur through the major portion of the area. This is true not only of many species of *Quercus* and *Hicoria* but also of the ultimate dominants with the highest requirements, such as *Tilia*, *Acer*, and *Fagus*. Practically all three of the latter attain the northern and southern limits or approach them, while *Fagus* is found all along the main body of the forest, *Acer* reaches the true prairie along the Missouri, and *Tilia* has

persisted still farther west. Such postclimax genera as *Betula, Fraxinus, Juglans,* and *Ulmus,* moreover, are widespread, maintaining the same general relation in all the associations. Finally, there is also great unity in the shrubby and herbaceous undergrowth, many species occurring from the Atlantic Coast to the Missouri, well beyond the limits of the climax climate.

The threefold differentiation of the formation has been chiefly a consequence of the climatic influence of the Appalachian system in the East and of the steady decrease in rainfall toward the West. The one has produced a grouping of dominants of relatively restricted range, such as *Castanea, Liriodendron, Quercus prinus* and its relatives, while the other has transferred the dominance to *Quercus* and *Hicoria,* which make somewhat smaller demands. In accordance with these facts, it is necessary to recognize three related associations, namely: (1) maple-beech, (2) oak-chestnut, and (3) oak-hickory. A further reason of great significance is that the deciduous climax has been the scene of a remarkable evolution of arboreal species and this has played an inevitable part in the structure of the associations.

The Maple-Beech Forest.—This is regarded as the typical association of the climax, because of the greater requirements of the dominants and their smaller number and of its greater similarity to the old-world forest. It characterizes the more humid and cooler northern and eastern portions of the climax area, and the two major dominants, *Acer saccharum* and *Fagus grandifolia,* are the most tolerant of shade. Although beech is theoretically the ultimate dominant, the requirements of the two are so nearly the same that they are regularly associated on more or less equal terms. Other important dominants are *Betula lutea, Tilia americana, Quercus rubra, Q. alba, Q. bicolor, Liquidambar styraciflua, Castanea dentata,* and *Liriodendron tulipifera.* All but the first two are more important in their respective associations, and their abundance increases in the corresponding ecotone. A frequent constituent is the hemlock, *Tsuga canadensis,* which has much the same requirements as the maple and beech and is often found associated with both but the latter especially.[122,123,187] It is, however, regarded as a relict of a former southward extension of the pine-hemlock forest, owing to its preference for cool north slopes or deep valleys, and not as a member of the climax proper (Fig. 253). Ash, elm, red maple, walnut, and other species of birch likewise occur with beech and maple, but they are considered as members of a subclimax stage belonging to the hydrosere.[368]

The general effect of fire in the maple-beech association is to develop or maintain a subclimax of oak-hickory. This is essentially a preclimax, since the oaks and hickories are more xeroid and are found throughout the association on hills, drier slopes, and on lighter soils as the subclimax stage of the xerosere. To the north and east, however, where pines occur

in abundance, the rule obtains and a burn subclimax of one or more species of jack pine or similar scrub pines develops. Along the contact with the pine-hemlock forest, this is regularly the jack pine proper, *Pinus banksiana,* where it is present, but much the most significant communities of this type are found from the New Jersey pine barrens south and westward along the coast to Texas. A number of species are concerned, ranging from *P. rigida, echinata,* and *virginiana* in the north to *P. echinata, tœda,* and *palustris* along the south Atlantic and Gulf coasts, to eastern

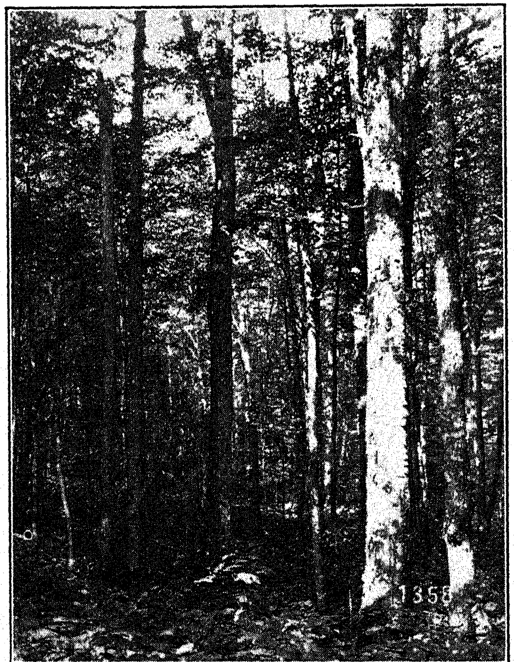

Fig. 253.—Typical hardwood forest with undergrowth of young beech and sugar maple under the parent trees, New York. *(Photo by courtesy of U. S. Forest Service.)*

Texas. The extent of this great pine belt has naturally led to the assumption that it is climax in nature, but its ecological character, as well as actual successional studies at widely separated points, leaves little or no doubt that it is essentially a fire subclimax.[335,576a,603]

Probably no other forest climax in North America exhibits such a wealth of societies as the deciduous forest. A large number of these range throughout from east to west, though their extension from north to south is not so great. There is a considerable number of small trees such as *Carpinus, Ostrya, Prunus, Cornus florida, Acer, Sassafras, Cratœgus,* and *Alnus,* while shrubby species of the upper and middle layers are usually much more abundant. The chief members of the upper shrub

layer, which is often merged with *Ostrya*, *Cornus*, etc., are *Hamamelis*, *Zanthoxylum*, *Amelanchier*, *Pyrus*, *Rhus*, *Ilex*, and *Viburnum*. Lower species of the last two are frequently associated with *Cornus*, *Corylus*, *Rubus*, *Rhus toxicodendron*, *Symphoricarpos*, etc.[46] In mountain regions, members of the heath family, *Oxydendron*, *Vaccinium*, *Kalmia*, and *Rhododendron*, often become important or characteristic.

The herbaceous societies constitute three or four aspects, of which the vernal and autumnal are the most striking. The vernal societies make most of their growth while the canopy of leaves is still somewhat open, and contain many species with well developed underground parts that promote early flowering. Among the most important of these are *Erythronium*, *Sanguinaria*, *Claytonia*, *Dicentra*, *Uvularia*, *Trillium*, *Arisæma*, *Anemone*, *Anemonella*, *Isopyrum*, *Viola*, *Aquilegia*, *Smilacina*, *Polygonatum*, *Geranium*, and *Phlox*, together with *Orchis*, *Cypripedium*, and other orchids. The summer aspect is usually characterized by such shade plants as *Impatiens*, *Laportea*, *Urtica*, *Sanicula*, *Osmorhiza*, etc., while the autumn is marked by a host of composites, especially *Aster*, *Solidago*, and *Liatris*. These attain their best expression in more open woods, especially of the oak type, where the first two genera may each be represented by a half-dozen species. A striking feature of the woodland societies is the relative abundance of genera with spiny or hooked fruits, such as *Agrimonia*, *Desmodium*, *Phryma*, *Lappula*, etc.

The Oak-Chestnut Forest.—The characteristic dominants of this association are the chestnut, *Castanea dentata*, the chestnut-oak, *Quercus prinus*, scarlet oak, *Q. coccinea*, and tulip tree, *Liriodendron tulipifera*. The red oak, *Q. rubra*, and white oak, *Q. alba*, are frequent associates, as well as *Liquidambar* and *Hicoria ovata*. It is in this association that the number of species of trees reaches a maximum, with a corresponding variety in the composition of the community. Like the other two associations, it has been much modified by fire and cutting where it has not been cleared for cultivation, but it has been further changed in the last two decades by the ravages of the chestnut blight, which has killed this dominant over most of its range.

This association lies in contact with the maple-beech on the north, and a more or less broken tongue of the latter extends southward along the Appalachian axis. On the west it is bordered by the oak-hickory forest, though in the Mississippi Valley the two are more or less separated by a broad belt of swamp forest.[533] In the Piedmont region of the Southeast this community passes into one composed of oak-hickory and pines that stretches to the coast, the subclimax pines often appearing to be a true climax where fire has more or less completely removed the oaks. Through the region of the oak-chestnut forest, the oak-hickory community also represents a preclimax characteristic of drier sites or thinner soils. In its most xeric form it is composed of the post oak, *Q.*

stellata, and blackjack, *Q. marilandica*, and recurs through the major part of the entire formation. The pine subclimax is likewise a preclimax, in which one species is regularly dominant; this may be loblolly pine, *Pinus tæda*, short-leaf pine, *P. echinata*, pitch pine, *P. rigida*, or long-leaf pine, *P. palustris*, with more or less *P. virginiana*, *serotina*, or *caribæa*, according to the region (Fig. 254).

Coastal and fluvial swamps from Virginia to Texas exhibit a typical forest community that is postclimax in nature, though it is actually

FIG. 254.—Longleaf pine (*Pinus palustris*), in Alabama. (*Photo by courtesy of U. S. Forest Service.*)

subclimax in the hydrosere. Its most striking dominant is the swamp cypress, *Taxodium distichum*, or the sour gum, *Nyssa aquatica*, though these frequently occur as codominants. The transition to the climax is marked by the water oak, *Quercus nigra*, sweet gum, *Liquidambar*, swamp oak, *Q. michauxii*, or live oak, *Q. viginiana*. Farther north these dominants mix with the sycamore, *Platanus occidentalis*, ash, elm, silver maple, etc., which constitute a postclimax of the maple-beech and oak-hickory associations.

The Oak-Hickory Forest.—The major dominants of this association are red oak, *Quercus rubra*, black oak, *Q. velutina*, white oak, *Q. alba*, and bur oak, *Q. macrocarpa*, shellbark hickory, *Hicoria ovata*, and mockernut,

H. alba, with pecan, *H. pecan*, in the southern portion (Figs. 31 and 33). A number of other species play an equally important part in more restricted regions or are found more or less scattered throughout. Such are scarlet oak, *Quercus coccinea*, willow oak, *Q. phellos*, laurel oak, *Q. imbricaria*, *Q. muhlenbergii*, *Q. falcata*, *Q. texana*, pignut, *Hicoria glabra*, and bitternut, *H. cordiformis*. Two other oaks, *Q. stellata* and *marilandica*, are frequent associates, but they belong properly to the subclimax. Dominants from the other associations are abundant in the respective ecotones and some occur more or less widely through it, particularly *Acer saccharum* and *Tilia americana*. In addition, this climax regularly

Fig. 255.—Mixed forest of white oak, shagbark and pignut hickory, etc., in winter, in northern Indiana. (*Photo by courtesy U. S. Forest Service.*)

forms mixtures with the postclimax dominants of lowlands, such as the swamp oaks, red gum, *Liquidambar*, ash, elm, walnut, etc. (Fig. 255).

The oak-hickory forest is much more interrupted than the two related associations, owing to the intrusion of the prairie through its entire length from Canada to the Gulf of Mexico. On the west, it stretches from southeastern Minnesota to central Indiana and thence southwestward through southern Illinois and Missouri to eastern Oklahoma and Texas. It is abundant in southern Michigan, but it regularly alternates there with the maple-beech forest, which occupies the better soils. This same preclimax relation obtains through much of Indiana and Ohio and recurs practically throughout the entire deciduous formation where soil or slope exposure delays the development of the climax or fire destroys the

latter. It reaches far out into the prairie climax, though with the dominants steadily dropping out; in southeastern Nebraska, most of the major dominants are present, but the majority disappear in the first hundred miles and only one, *Quercus macrocarpa*, persists into northeastern Wyoming.[5,401] In the Southeast, the oak-hickory climax lies between the oak-chestnut association and the coast, but it has been replaced over much of this region by the fire subclimax of pines. The relict areas of beech in this region suggest that the oak-hickory community is here subclimax to an original maple-beech association.[576a,576b,576c]

Extensive areas of oaks, the Cross Timbers, occur as two massive belts through central Texas and extend more or less broken into Oklahoma.[526] These have usually been regarded as portions of the oak-hickory forest, but this is not true in the climax sense. They are composed almost wholly of post oak and blackjack, *Q. stellata* and *marilandica*, which are never true climax dominants. On careful examination, the cross-timbers have proved to be oak savannah, in which the grasses are the actual climax dominants. The soil is typically light and sandy, and the oaks are relicts from a former moist phase of the climatic cycle that have been able to maintain themselves against the competition of the grasses by virtue of the favorable chresard of the sandy soil. In this prairie climate, the oaks constitute a postclimax, since the climax forest would return in the event of a shift to a wetter climate. Conversely, the post oak and black jack constitute a subclimax in the succession within the mass of either of the three climax associations and, hence, a preclimax that would become dominant in the case of a swing to a drier climate.

The relation of the oak-hickory association to the subclimaxes in swamps and in burned areas is much the same as that indicated for the oak-chestnut forest. The dominants of the cypress swamp are essentially identical and the development into the climax takes place through the agency of practically the same species. This is also true, in a large measure, for the pine subclimax, though the northerly species have disappeared, leaving the widely distributed *Pinus echinata*, *P. tæda*, *P. palustris*, and the more southern *P. caribœa*. Through the northern part of the association, the associes of river bottoms consists of ash, elm, silver maple, walnut, and sycamore or cottonwood, as in the case of the other two associations (Fig. 32).

THE GRASSLAND CLIMAX

The Prairie

Extent and Nature.—The grassland or prairie formation is the most extensive and the most varied of all the climaxes of the North American continent. It ranges from northern Saskatchewan and Alberta and cen-

tral British Columbia to the highlands of central Mexico and from western Minnesota and Iowa to the coast of California and Lower California. In the form of the closely related subclimax it extends eastward to Indiana, and still further outposts are to be found in Ohio and Michigan. The eastern half is massive and is broken only by the fringing forests of river valleys, but the western is greatly interrupted by the many mountain ranges and its continuity much reduced in consequence. In altitude the prairie ranges from the seacoast in Texas and California to the grassy parks of the Rocky Mountains at 7,000 to 9,000 feet, though the upper limit here rarely exceeds 6,000 feet and elsewhere it is usually much lower.

The prairie owes its character to the dominant grasses, most of which assume the life-form known as *bunch grass*. In general correspondence with the rainfall, these fall into three well-defined groups based upon stature and known as *tall grasses*, *mid-grasses*, and *short grasses*, which are more or less characteristic of the various associations. With the grasses are associated a much larger number of subdominant forbs, which often give the prairie a distinctive tone and fall into mixed societies in accordance with the season or aspect. Woody plants are few in species and altogether unimportant because of their low stature, except where disturbance, and especially grazing, has given them an advantage. Over large areas of climatic grassland, sagebrush, mesquite, or similar shrubs are abundant and often appear to be controlling, but these are almost invariably responses to overgrazing. Similar savannahs of mixed trees and grasses are frequent around the margin of the formation, as well as where it lies in contact with montane or deciduous forest, or with woodland, but these are primarily postclimax areas left in consequence of climatic changes (Fig. 234).

Like the deciduous forest, the prairie finds its nearest relative in Eurasia, the steppes of Russia and adjacent Asia being prairies in all essential respects. They are to be regarded as descendants of one original grassland, identical in their basic climatic and ecological relations but differing considerably in the component genera and much more in the species. There is also a certain degree of phylogenetic relationship with the pampas of South America and at least a significant interchange of species between the grassland and the tundra, alpine as well as Arctic.

The grassland climax lies in contact with more formations than any other on the continent. The sole complete exception is the tundra, though the contact with the subalpine, boreal, and lake forest is slight. The outstanding relations are with the deciduous and montane forests, with the woodland climax, and with the three scrub climaxes—sagebrush, chaparral, and desert scrub. The main body of the prairie touches the deciduous forest throughout the entire length of its greatly indented western border and comes in contact with the montane forest along the

front ranges of the Rocky Mountains. In New Mexico and Arizona, it usually confronts the woodland climax above, as also in the southern portion of the Great Basin, while below it alternates and mingles with the desert scrub and sagebrush. In California it is bordered by the coastal sagebrush and chaparral above, and in the Northwest it lies in contact with the montane or transition forest.

In general, the climax prairie lies west of a rainfall of 20 to 25 inches in the north and of 35 to 40 inches in Texas, with an average of about 33 inches at the middle. There is a general correspondence between the main body of the formation in the Middle West and the region in which 70 per cent of the annual precipitation comes between Apr. 1 and Sept. 30, but this is less significant than it seems. As a consequence of its peculiar life-form, grassland occupies wide limits between climax forest and xeric scrub or woodland. In terms of rainfall, this means a range of 35 to 10 inches or less, with great differences in distribution likewise. From a summer precipitation of 70 to 80 per cent of the annual amount in the Middle West, the percentage drops to 40 to 50 in Arizona and to 10 to 20 along the Pacific Coast, the rainfall changing from the summer to summer-winter and then to the winter type. The primary correlation is with rainfall sufficient in amount and frequence at a time of favorable temperatures to permit the growth and reproduction of the grass dominants. The closeness of this correspondence is exemplified by winters of two rainfall maxima in California, during which the grasses bloom in December and again in the spring. The wide range of temperature for the grassland is shown by the fact that it meets winter extremes of −50°F. or lower in Canada and summer ones of 120°F. in the south; the season in the north is but 3 to 4 months; while in the south and along the Pacific Coast frost may occur but rarely if at all. Throughout this vast area, however, the grasses pass a long period in the resting stage, in relation to low temperatures in the north and low rainfall in the south and west.

The unity of the grassland climax is evidenced, in the first place, by the large number of genera that occur as dominants more or less throughout, such as *Stipa*, *Agropyron*, *Kœleria*, *Poa*, *Sporobolus*, *Elymus*, and *Bouteloua*. Even more significant is the occurrence of such species as *Stipa comata*, *Kœleria cristata*, *Agropyron smithii*, *Poa scabrella*, *Elymus sitanion*, *Aristida purpurea*, and *Bouteloua gracilis* in all or nearly all the associations. Other dominants, like *Andropogon scoparius*, *furcatus*, and *saccharoides*, *Elymus canadensis*, *Sporobolus cryptandrus*, and *Bouteloua racemosa*, are found in three or four of the six climax associations. The genera of the subdominants are also largely the same through the entire formation, though it is only exceptionally that the same species grows in the different associations. The unity of the climax is further indicated by the mixed prairie with its short grasses and mid-grasses, which serves to connect the true prairie with the bunch-grass prairies and the desert

plains. Even the Pacific prairie of California, which is today completely shut off by desert and mountain from its related associations, has practically all the dominant genera and some of its species in common with them.

The True Prairie.—The dominants of this association are mid-grasses of both the sod and the bunch life-form. The major dominants are *Stipa spartea*, *Sporobolus asper*, *Andropogon scoparius*, *Kœleria cristata*, *Agropyron smithii*, and *Bouteloua racemosa*, often with *Andropogon furcatus* and *nutans* from the subclimax and *Stipa comata* from the mixed prairie. Such short grasses as *Bouteloua gracilis*, *B. hirsuta*, and *Bulbilis dactyloides* are not infrequent, but they constitute relict areas of little extent, except where favored by overgrazing. *Agropyron* is a sod former, *Andropogon scoparius* and *Bouteloua racemosa* are intermediate in habit in this community, while the other major dominants are bunch grasses. *Stipa spartea* and *Sporobolus asper* are the two most characteristic dominants, since they do not occur as such in any other association[401] (Fig. 230).

Cultivation has almost completely removed the true prairie over most of its area and its original limits are correspondingly difficult to determine from the small and widely scattered fragments.[530,574] It occupies a fairly distinct belt between the subclimax and mixed prairies, reaching from Manitoba into central Oklahoma. To it belong southern Manitoba, western Minnesota, and the eastern part of the Dakotas, eastern Nebraska and western Iowa, east-central Kansas and Oklahoma. Because of the gradual change of climate from the subclimax to the mixed prairie, the influence of topographic features, and the all but complete removal of the original cover over large areas, the exact limits of the several prairies can never be set, and the boundary lines drawn on any map can be only general approximations.

This association is most closely related to the mixed prairie and somewhat less closely to the subclimax prairie with both of which it is in contact, as well as being nearly enclosed by them. It forms a broad ecotone with the first on the west and with the second on the east, in which the respective dominants meet on equal terms. Several of its dominants are more abundant in the mixed prairie and this is strikingly the case with the relict short grasses. The ecotone on the east has been broadened by the much greater destruction of the bunch grasses during the period of settlement and the consequent encroachment of the coarse bluestems, *Andropogon furcatus* and *nutans*, which have spread well into the climax itself.

The true prairie contains a larger number of striking societies than any other association of the grassland. The subclimax prairie receives more rain, but this advantage is offset by the larger demands of the tall grasses and their overshading action, while the number in the mixed prairie and other associations is restricted by the lower rainfall. The dominant grasses and the subdominant forbs are in active competition for water

and, to a smaller extent, for light and nutrients, but, as a rule, the grasses have a decisive advantage and societies can flourish only where there is enough water for both. Competition between societies is avoided in a considerable degree by their flowering at different seasons, as a result of which three characteristic aspects develop. The number of subdominants in each is usually large, and hence the societies are mixed, consisting of several fairly abundant species.[225] The spring aspect is marked especially by *Astragalus crassicarpus*, *Baptisia bracteata*, *Callirhoe alcœoides*, *Phlox pilosa*, *Sisyrinchium angustifolium*, species of *Lithospermum*, *Viola pedata* and *pedatifida*, *Anemone caroliniana*, *Tradescantia virginiana*, etc. The summer aspect exhibits mixed societies of two or more of the following, together with a host of less important ones· *Psoralea tenuiflora* and *argophylla*, *Erigeron ramosus*, *Amorpha canescens*, *Petalostemon candidus* and *purpureus*, *Glycyrrhiza lepidota*, *Brauneria pallida*, and *Helianthus rigidus*. The societies of late summer and autumn are composed chiefly of composites, largely species of *Solidago*, *Aster*, and *Liatris*, together with *Kuhnia*, *Artemisia*, *Carduus*, *Helianthus*, and *Vernonia* (Figs. 4 and 8).

The Subclimax Prairie.—As the name indicates, this is the prairie that lies within the climate of the deciduous forest or along its broad margin. It consists of tall grasses, often 6 to 8 feet high and belonging mainly to the sod-forming type.[440] Over most of the area the major dominants are the three species of *Andropogon*, *viz. furcatus*, *nutans*, and a tall form of *scoparius*. With these occur more or less abundantly *Elymus canadensis* and *Panicum virgatum*, and two mid-grass dominants of the true prairie, namely, *Stipa spartea* and *Sporobolus asper*.[471] In the south, there are, in addition to the three species of *Andropogon*, a large number of regional dominants, such as *A. glomeratus*, *A. ternarius*, *Erianthus*, *Elionurus*, *Heteropogon*, *Trachypogon*, and *Paspalum*.

This community is necessarily regarded as an associes because of its presence in a forest climate, as well as by reason of the fact that shrubs and hardwoods are slowly invading it where the disturbance due to man is not too great. It is evident, however, that the utilization of both communities by man has reached the point where they will remain in fair equilibrium until one or the other is further removed. The subclimax prairie in general represents an eastward movement of the climax prairie into the region of the deciduous forest as the latter retreated in consequence of reduced rainfall. The reciprocal withdrawal of the grasses did not take place, partly because they adjusted themselves to the increasing rainfall, but chiefly because their competition with the seedling trees prevented anything more than an exceedingly slow advance of the latter. As a consequence, this subclimax has persisted for thousands of years as a great grassland triangle in the heart of the oak-hickory forest. During this time, small portions of it along the margin and at the tip have been

regained by forest, as the relict outposts of prairie in Ohio and Michigan show. To the southward the forest presented a solid front and the subclimax prairie is reduced to a narrow belt between forest and coastal prairie, to which additions have been made as a result of fire and lumbering.

The societies of the subclimax prairie are essentially those of the true prairie, reinforced by additions from the deciduous forest and the meadows included in it. The number of species of composites is considerably larger, especially of *Aster* and *Solidago*, and some have come to serve as distinct indicators of the subclimax, notably *Silphium terebinthinaceum*, *laciniatum*, *trifoliatum*, and *Helianthus orgyalis*.

The Coastal Prairie.—From its general location near the Gulf of Mexico, this association has the highest rainfall of any, though this is partly offset by a longer season and greater evaporation. The midgrasses tend to approach the tall grasses in stature, and the number of dominants is likewise increased. A significant feature over much of its area is the presence of short grasses of the genera *Bouteloua*, *Bulbilis*, and *Hilaria*, producing a resemblance to mixed prairie. The latter differs, however, inasmuch as the short grasses are climatic dominants, while in the coastal prairie their presence is due primarily to overgrazing. They are more abundant in the west and are moving eastward in the wake of grazing, the eastern portion consisting of the original tall grasses alone. A similar result has taken place in the subclimax prairie of eastern Kansas, where *Bulbilis*, in particular, has spread far eastward and frequently forms a pure stand in pastures.

The major dominants of the coastal prairie are *Andropogon saccharoides* and *Stipa leucotricha;* the latter, in particular, serves to distinguish it from the true prairie to the north and the mixed prairie on the northwest. Even more than *Stipa spartea*, it finds its limits within the association to which it gives character. In addition to the three andropogons from the subclimax prairie, there is a large number of regional dominants in the southeastern portion especially, notably *Elionurus*, *Trachypogon*, *Erianthus*, *Paspalum*, *Sporobolus*, and *Heteropogon*. The short grasses are *Bulbilis dactyloides*, *Hilaria cenchroides*, *Bouteloua trifida*, *texana*, and *hirsuta*, together with the slightly taller *Cenchrus tribuloides* and *Panicum obtusum*. In the number of dominants and the wealth of genera and species of grasses, this association excels all others of the grassland formation.[526]

The closest relationship of this community is with the true prairie, though the line of contact with this is narrower than with either the mixed prairie or the desert plains. Its major dominants belong to the same genera and it bears a similar relation to the subclimax associes, into which it passes on the east. It possesses *Stipa*, *Bouteloua*, *Bulbilis*, and *Aristida* in common with the mixed prairie, but the first alone as a climax

dominant. The short grasses *Hilaria, Bouteloua trifida* and *texana* are derived from the desert plains, but these two associations have no climax dominant in common owing to the marked difference in rainfall. The societies belong to much the same genera as those of subclimax and true prairie, but there are naturally more species of southern origin.

The Mixed Prairie.—This community owes its name to the fact that the climax comprises both mid-grasses and short grasses, on more or less equal terms. The major dominants of the widest distribution are *Stipa comata, Sporobolus cryptandrus, Agropyron smithii,* and *Kœleria cristata* of the mid-grasses, and *Bouteloua gracilis* and *Bulbilis dactyloides* among the short grasses. Intermediate in stature are *Hilaria racemosa, Elymus sitanion, Bouteloua racemosa,* and *Aristida purpurea.* Additional short grasses of importance are *Bouteloua hirsuta, Carex filifolia* and *stenophylla,* and *Muhlenbergia gracillima,* while *Stipa viridula* is abundant in the north and *Stipa pennata* in the south (Fig. 232).

The mixed prairie covers by far the largest area of any of the grassland associations, stretching from northern Alberta and Saskatchewan through the Staked Plains of Texas and from central North Dakota and Oklahoma on the east to western Wyoming and eastern Utah and southwestward through northern New Mexico and Arizona to the Colorado Valley.[442,460] While it is not uniform through this vast extent, the presence of the major dominants over nearly all of it leaves no doubt of its unity. The chief modification is a result of overgrazing, in consequence of which the mid-grasses are often little in evidence and the short-grass plains thus produced appear to be climax in nature.[461] The next most important variation is due to the distribution of the many dominants, by which the composition changes from north to south particularly. While the four major mid-grasses, together with *Bouteloua gracilis* and *Aristida purpurea,* are found practically throughout, they vary much in importance and with the regional dominants form various combinations within the association. *Stipa viridula, Carex filifolia,* and *C. stenophylla* are largely restricted to the northern portion, *Bulbilis* and *Aristida* are most abundant in the middle region, and *Hilaria, Stipa pennata, Elymus sitanion,* and *Muhlenbergia gracillima* are wholly or largely southern. The closest relationships of this association are with the true prairie, with the desert plains and coastal prairie next, though it possesses several dominants in common with the Pacific prairie, in spite of the isolation of the latter.

The transition from the true to the mixed prairie is very gradual and the corresponding ecotone unusually broad. The best limit is set by the disappearance of *Stipa spartea* and *Sporobolus asper,* which are replaced in the mixed prairie by very closely related species, *S. comata* and *S. cryptandrus.* In Nebraska the relation is further disturbed by the extensive sandhill region, in which the high chresard favors a postclimax of tall grasses far beyond their proper climate. The societies of the mixed

prairie are largely derived from the true prairie, in the central portion, at least, and the decrease in the number and abundance of these also serves to mark the change from one association to the other. With the decrease in rainfall of 10 inches, the more mesic forbs disappear or are much reduced in stature or abundance, with the result that societies play a much less important part, especially in a rainfall of 15 inches or less. *Psoralea tenuiflora*, *Petalostemon*, *Tradescantia*, *Helianthus rigidus*, *Solidago missouriensis*, *Liatris punctata*, etc., persist over much of the area, especially in sandy soils or on broken hills with more available water, but more xeric subdominants from the west are now more important. Among these are *Aragallus lambertii*, *Sophora sericea*, *Malvastrum coccineum*, *Artemisia frigida*, *Gutierrezia sarothrae*, several species of *Astragalus*, *Pentstemon*, and *Opuntia*.

The Short-grass Subclimax.—Over a large portion of the mixed prairie, especially where rainfall and evaporation are less favorable, the mid-grasses are usually inconspicuous or even absent. As a consequence, such stretches were long regarded as a distinct climax, under the name of short-grass plains. During the last decade, evidence has been accumulated from various sources, which makes it clear that the dominance of the short grasses is a result of overgrazing. This greatly handicaps the taller grasses and correspondingly favors the short grasses; it has been so widespread and serious as to justify the impression that the short-grass plains are the most xerophytic climax of the grassland formation. Three sources of evidence have, however, combined to prove that it is a modified form of the mixed prairie. In all protected places, as well as in those where sandy soil or broken topography increase the water available, the mid-grasses still persist. Even more convincing evidence has been secured from exclosures fenced against cattle, in which the mid-grasses return in a few years. Finally, when the pressure of grazing is offset by normal or excess rainfall, the taller grasses are also able to compete with the short ones on equal terms or even to dominate them more or less completely. Under overgrazing, the subdominant forbs suffer even more than the mid-grasses, and the short-grass plains are often an almost unbroken sod of *Bouteloua* and *Bulbilis* (Figs. 231 and 235).

The Desert Plains.—This is the most xerophytic association of the grassland, stretching as it does from southwestern Texas through southern New Mexico and Arizona and northern Mexico. This is reflected in the stature, the true climax dominants being almost wholly species of *Bouteloua* and *Aristida*. In consequence, it most nearly resembles the short-grass subclimax of the Great Plains and is hardly to be distinguished from it in appearance when overgrazed. Its major dominants are *Bouteloua eriopoda*, *rothrocki*, *bromoides*, *gracilis*, and *hirsuta*; *Aristida divaricata*, *purpurea*, *californica*, and *arizonica*; and *Hilaria cenchroides*. The only mid-grass that belongs definitely to this group is *Muhlenbergia*

porteri, but there are a number of similar species that are found in sand, in depressions, or on rough slopes and are, hence, somewhat postclimax in nature. Of those the most important are *Bouteloua racemosa*, *Andropogon scoparius*, *A. saccharoides*, *Panicum lachnanthum*, *Heteropogon*, *Sporobolus cryptandrus*, *Eragrostis*, *Leptoloma*, etc. Most abundant of all, though to be regarded as a definite subclimax, is *Hilaria mutica*, which dominates extensive depressions or "swags" throughout the association, usually with a short grass, *Scleropogon*, as its associate (Fig. 256).

The chief contact of the desert plains is with the mixed prairie through its entire length on the north, and the two are mixed over a broad ecotone. Along the escarpment that rises from the Colorado Desert, it sweeps

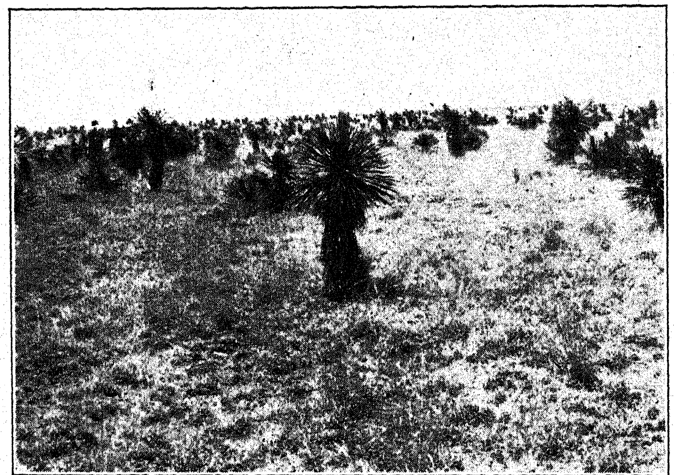

FIG. 256.—Desert plains grassland with *Yucca radiosa*, Empire Valley, Ariz.

northward and replaces the mixed prairie in this region of low rainfall. At its eastern limit it touches the coastal prairie and contributes to it most of its short grasses. The northern boutelouas, together with *Andropogon* and *Hilaria cenchroides*, constitute the upper belt in the foothills at 4,000 to 5,000 feet, where they regularly form savannah with several species of oaks. Owing to the dry subtropical climate, the major portion of this association is dotted with desert shrubs of the genera *Larrea*, *Prosopis*, *Acacia*, *Celtis*, *Ephedra*, *Flourensia*, *Opuntia*, etc., which are often so increased by overgrazing as to simulate a scrub climax.

Intensive overgrazing has also produced a subclimax of annual grasses chiefly of the genera *Bouteloua* and *Aristida*, and of annual forbs, which develop during the summer rains and cover most of the area at the lower elevations. Even more striking are the vast societies of winter annuals, which often stretch for many miles in successive pure stands. The

perennial societies of midsummer are represented largely by undershrubs, such as *Haplopappus*, *Gutierrezia*, *Psilostrophe*, and *Zinnia*.[213a]

The Pacific Prairie.—This association consists of mid-grasses of the bunch life-form and, hence, has much the same general appearance as the mixed and true prairies. This is enhanced by the fact that it has one dominant, *Stipa setigera*, which far overshadows all the others. Several other mid-grasses occur with it in sufficient abundance to serve as dominants, and to the north and along the seacoast *Stipa* becomes secondary or is entirely lacking. The most important of these are *Stipa eminens*, *Kœleria cristata*, *Poa scabrella*, *Melica imperfecta*, *Elymus sitanion* and *triticoides*, with species of *Danthonia*, *Bromus*, and *Festuca* under moister and cooler conditions, as along the coast, in the north, and at higher levels (Fig. 257).

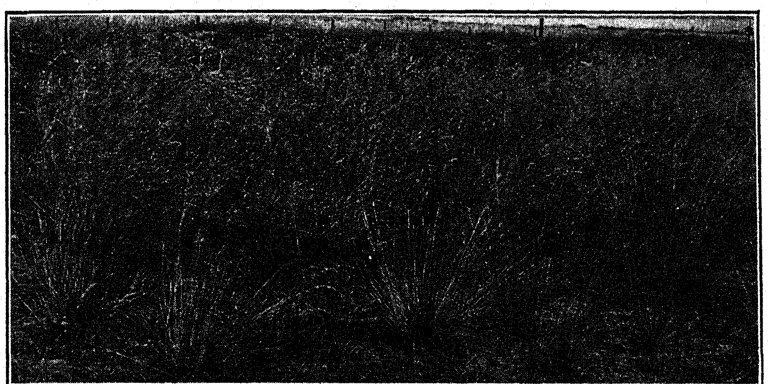

Fig. 257.—*Stipa setigera* consociation characteristic of the original bunch-grass prairie of California.

The native bunch-grass prairie of California has been so largely destroyed by overgrazing and fire that its reconstruction has required persistent search for relict areas. This has been so successful that it is now possible to determine its original area and composition and, in consequence, its contacts and relationships. Within the historical period, this grassland has been entirely confined to California and Lower California. Its closest affinities are with the bunch-grass community of the Palouse, with which it forms an ecotone in northern California. Today it is completely separated from the mixed prairie by the Sierra Nevada and the deserts of the Southwest, but relicts of *Bouteloua*, *Andropogon*, *Hilaria*, and *Aristida* in southern California and the presence of *Stipa eminens* and *speciosa* in Arizona and New Mexico attest a former connection through the Mohave and Colorado deserts. This is also supported by the presence of many of its species as relicts in the mountains in and about Death Valley, and the certainty

of this connection is evidenced likewise by a large number of California forbs and shrubs that still persist in the mountains of Arizona.

The native bunch grasses once occupied all of the Great Valley of California as well as the valleys and lower foothills of the Coast and Cross ranges and of the Sierra Nevada. They have been more or less completely dispossessed by annual grasses introduced from Europe, as a consequence of overgrazing in a region with a long, dry season. This has resulted in maintaining a successional stage of annuals of such permanence as to simulate a subclimax, composed chiefly of *Avena fatua*, *Bromus maximus*, *rubens*, and *hordeaceus; Hordeum maritimum*, *murinum*, and *pusillum;* and *Festuca myuros* and *megalura*. In the case of *Avena* especially, the cover is so tall and dense as to have suppressed many of the perennial forbs and the societies of the grassland are largely winter annuals, the species more numerous than in Arizona but many of them identical. Among the most important genera are the following: *Eschscholtzia*, *Bœria*, *Orthocarpus*, *Lupinus*, *Lotus*, *Mimulus*, *Gilia*, *Phacelia*, *Nemophila*, *Layia*, *Hemizonia*, and *Madia*, while the perennials belong to *Brodiœa*, *Calochortus*, *Allium*, *Delphinium*, *Dodecatheon*, *Sisyrinchium*, *Pentstemon*, etc.

The Palouse Prairie.—This resembles the Pacific prairie in the life-form of the grasses and in its relation to winter precipitation, but the major dominants are quite different. These are *Agropyron spicatum*, *Festuca ovina*, and *Elymus condensatus*, while it possesses *Poa scabrella*, *Kœleria cristata*, and *Elymus sitanion* in common with the Pacific and mixed prairies, and *Stipa comata* and *Agropyron smithii* in common with the latter.[393] In composition, it resembles the latter more nearly, and this is reflected in the fact that they alternate and mingle along a wide zone of contact. On the other hand, this association stands close to the bunch-grass prairie of California in its water relations and in the absence of short grasses, and the two lie in touch through the valleys of northern California. It attains its best development on the rugged hills of the great wheat-producing region known as the Palouse but is characteristic, in general, of eastern Washington and Oregon, southern Idaho, and northern Utah[559] (Fig. 258).

Over most of its area, this prairie has been replaced by two communities that owe their advantage to overgrazing and, in the case of the annuals, to fire also. So abundant is the sagebrush throughout the major portion that this whole region has been assigned to the sagebrush climax, but the study of relict and protected areas, especially experimental exclosures, proves that the grasses are climax and that they again assume dominance when grazing is much reduced or eliminated. A more recent change has been the replacement of the grasses by annuals, with results similar to those found in California. The most important invader is *Bromus tectorum*, frequently with other species of the same

genus, while two annual forbs, *Sisymbrium altissimum* and *Lepidium apetalum*, are often of equal and sometimes greater importance. The societies of this association are drawn largely from the two adjacent prairies, but a number of them are peculiar to it. Especially characteristic ones are constituted by the composites, among which *Balsamorrhiza sagittata*, *Wyethia amplexicaulis*, *Gaillardia aristata*, *Achillea millefolium*, and *Agoseris grandiflora* are the more important.

FIG. 258.—Bunch-grass prairie of *Agropyron* and *Elymus* in contact with sagebrush in Idaho.

THE WOODLAND CLIMAX

Extent and Nature.—The woodland formation is composed of small trees capable of forming a canopy and, hence, of constituting a real though low forest under the proper conditions. Typically, the woodland consists of small trees 20 to 40 feet high and belonging to the three genera, *Juniperus*, *Pinus*, and *Quercus*. While these vary widely in leaf character, they agree in being evergreen and xerophytic as well as more or less subtropical in temperature relations. They form fairly dense crowns and in favorable situations make a continuous canopy and a fairly dense shade. Practically all the species may vary from trees 30 to 50 feet tall to shrubs of 10 to 20 feet and, in some cases, to bushes of even smaller stature. As trees they often give the appearance of being integral parts of the forest communities in which they occur, while in the form of shrubs and bushes they are equally at home in chaparral. The consequence is that the same species may appear as an important if not abundant constituent of forest, woodland, or chaparral, and its proper rôle becomes difficult of determination.

The woodland formation is essentially southwestern, xeric, and subtropical, though at the upper altitudes of 6,000 feet or more it extends

into the region of winter snow. It finds its best expression on the high plateaus of the Colorado Basin, but it occurs from the Edwards Plateau and the Davis and Guadalupe Mountains ofwestern Texas through northern Mexico to Lower California. It extends northward along the foothills in New Mexico and Colorado to southwestern Wyoming and thence westward through Utah and Nevada to northern California, its outposts reaching the outer Coast range in the south-central part of the state. At its lower limit it lies in touch with the grassland formation and especially the sagebrush savannah, while in California it is in contact with the chaparral, with which it forms extensive mixtures. Along its upper margin it meets the yellow-pine consociation of the southern Rocky Mountains and the desert ranges.

Fig. 259.—Pine-oak woodland of the foothill region of California.

As an essentially forest community in a warm, dry region, the woodland formation has suffered more from climatic desiccation than any other. In consequence, perhaps less than a fourth of it remains today in the climax condition with a closed canopy and a proper ground cover. Throughout most of its area it is a more or less open savannah in climatic mixed or bunch-grass prairie or, more rarely, in the desert plains. The true climax areas are found only at the upper altitudes, especially on the Colorado Plateau and in the higher ranges of southern Arizona and northern Mexico.[483] Over much of the lower region it is reduced to a single species of *Juniperus*, which appears as a low shrub or bush. This type of savannah has been greatly extended in the last half century in consequence of overgrazing and the carriage of the seeds by sheep and birds (Fig. 259).

The woodland climax falls into three divisions or associations, namely, the *Quercus-Juniperus*, the *Pinus-Juniperus*, and the *Pinus-Quercus*.

The first of these is southern and southeastern in position and probably represents the original mass of the formation. The second is central and typical, while the last is found in California and Lower California. The first two are in contact with each other over a long distance but are readily distinguished by the presence of *Juniperus pachyphlœa* and the evergreen oaks in the former. The California association is separated from the other two by the Colorado and Mohave deserts and the Sierra Nevada, and the dominants mix but slightly, the contact being maintained only by *Pinus monophylla* and *Juniperus californica*. The major dominants of the oak-juniper woodland are *Quercus reticulata, Q. hypoleuca, Juniperus pachyphlœa, J. occidentalis monosperma, J. sabinoides, Pinus cembroides,* and *P. edulis*. The piñon-juniper association is dominated by *Juniperus o. monosperma, J. c. utahensis, Pinus edulis,* and *P. e. monophylla,* while the pine-oak woodland is essentially all savannah today, in which the important trees are *Pinus sabiniana, Quercus douglasii, Q. wislizeni, Juniperus californica* and its variety *utahensis, J. occidentalis, Pinus edulis,* and *P. cembroides,* often single or combined in groups of two or three.[213a]

THE CHAPARRAL CLIMAX

Extent and Nature.—The chaparral formation is characterized by shrubs of the same general life-form and, for the most part, of similar systematic relationship. In comparison with forest it is xeroid in character but less so than sagebrush and desert scrub, which resemble it in physiognomy. Climatically, it represents the intermediate condition between grassland and forest, and it actually occupies this position between these two climaxes along much of their line of contact. It is better developed in the south than the north and attains its best expression in subtropical regions that incline toward desert in nature. It is peculiarly responsive to fire, which has left an impress on its form at the same time that it has modified its area. Practically all species of the chaparral, as of the scrub generally, produce sprouts readily from the roots when the tops have been burned or cut. As a consequence, frequent burning reduces their stature and modifies their form by the production of several stems in place of a single trunk. An effect of even greater significance is the fact that fire, which is the great enemy of forest, regularly favors chaparral in its competition with grassland, except where it occurs practically every year.

Geographically, chaparral is a western formation, reaching its typical development on the foothills of the southern Rocky Mountains, the interior ranges in Utah and Arizona, and on those of the Sierra Nevada, Coast Ranges, and Cascade Mountains of the Pacific Slope.[112] In reduced form it extends northwestward from the Black Hills to the Blue Moun-

tains, and as a narrow subclimax band it borders much of the western edge of the deciduous forest. Somewhat similar subclimaxes of dwarf oaks, called *shinnery*, cover considerable areas of sandhills and river dunes through the southern portion of the mixed prairie (Fig. 90).

This climax resembles forest in the wide range of rainfall in which it occurs, its correlation with the latter being much affected by relatively high temperatures and evaporation. In the Rocky Mountains the chaparral lies between 15 and 20 inches of rainfall; in southern California it ranges from 10 to 20 inches; and in northern California and adjacent Oregon it occurs on dry slopes under 50 to 60 inches. The occurrence of chaparral in 10 inches of rainfall is possible only where evaporation is reduced by the proximity of the ocean, and under 50 inches only where insolation greatly increases water loss. This community reaches its greatest height and density where the summer temperatures are high and, in particular, under a winter rainfall with no protracted cold period.

The lower contact of chaparral is typically with grassland, but in the southern half of California, as well as some parts of the Great Basin, it is with sagebrush. The upper portion touches woodland or the yellow-pine consociation and because of their open nature often forms a layer beneath them. Its constituent shrubs invade talus slopes or rocky soils more readily than grasses and in such situations it may long persist as a postclimax in grassland.

The Petran Chaparral.—This association reaches its best development in Colorado, northern New Mexico, and eastern Utah, where most of the climax areas are to be found. As a subclimax much poorer in species and reduced in stature, it may be found along foothills from South Dakota to Texas and from the north to the south of the Great Basin. The association attains its best development between 5,000 and 8,000 feet, and the climax portions are restricted to this zone.

The major dominants of the widest extent are *Quercus gambelii*, *Q. undulata*, *Cercocarpus parvifolius*, *Rhus trilobata*, *Prunus demissa*, and *Amelanchier alnifolia*. In the Southwest, *Robinia neomexicana*, *Fendlera rupicola*, *Ceanothus ledifolius*, *Peraphyllum ramosissimum*, and *Philadelphus gordonianus* are often of equal or even greater importance, while in the mountains of central Arizona, *Arctostaphylos pungens* and *Ceanothus cuneatus* appear as dominants that mark the transition to the Sierran chaparral.

The Coastal Chaparral.—This association is much more massive than the Petran but covers a smaller territory. It differs, also, in consisting chiefly of evergreen or sclerophyll shrubs, only one of the major dominants, *Quercus dumosa*, being deciduous. The number of dominants and the continuity of the cover are greatest in California and adjacent Lower California, and both features diminish to the north. Apart from the fact that the one is typically evergreen and the other deciduous, the

two associations resemble each other closely in the form, height, and general relations, in the genera of the dominants, and in the essential character of the community.

The coastal association is best developed on the Coast and Cross ranges of middle and southern California and in northern Lower California. Though much reduced in species, it is still an important community as far north as southern Oregon. It extends eastward to the lower slopes of the Sierra Nevada and thence to southeastern California and adjacent Nevada and Arizona. Here it is reduced to *Ceanothus cuneatus greggii* and *Arctostaphylos pungens*, which range still farther eastward where they become merged in the Petran association. The climax proper is

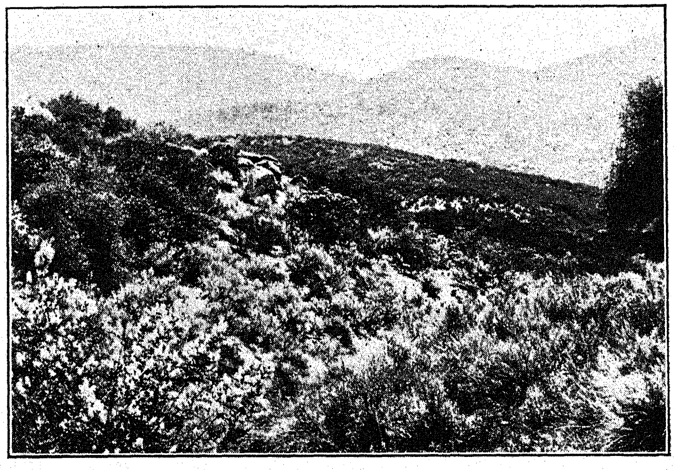

FIG. 260.—Coastal chaparral of *Adenostoma* and *Ceanothus* in California.

restricted chiefly to California, though even here extensive areas at the lower altitudes are subclimax (Fig. 51).[112] Subclimax chaparral also occurs in the lower portion of the montane zone as a fire community, but the species of the dominants are almost wholly different and the two subclimaxes are not directly related (Fig. 260).

The major dominants are *Adenostoma fasciculatum*, *Ceanothus cuneatus*, *C. oliganthus*, *C. spinosus*, and *C. divaricatus*, *Arctostaphylos pungens* and *tomentosa*, *Quercus dumosa*, *Prunus ilicifolia*, and *Rhamnus crocea*. There is a much larger number of minor and regional dominants belonging to the same genera, as well as *Rhus*, *Cercocarpus*, *Amelanchier*, and *Holodiscus*, which likewise occur in the Petran chaparral, where they are largely represented by the same species. In addition, the chaparral includes several species that properly belong to the coastal sagebrush of the next zone below.

THE SAGEBRUSH CLIMAX

Extent and Nature.—The sagebrush, *Artemisia tridentata*, is so striking in color and form as to give the appearance of a climax to wide stretches that belong climatically to the grassland formation. As a distinctive feature of the landscape, it is more or less abundant from the Black Hills to southern British Columbia, southeastern California, and northern Arizona. As a climax, however, it is confined essentially to the central portion of the Great Basin, from middle Utah to southern Idaho and Oregon, northeastern California, and Nevada.[213a,531]

The sagebrush climax owes its character to the dominance of low shrubs or bushes, and is to be regarded as a desert scrub that has migrated widely since its early development in the Southwest. It differs from desert scrub, mesquite, and chaparral, however, in the fact that the dominants are practically all shrubby adaptations of families predominantly herbaceous, particularly the asters and goosefoots. This fact explains, in large measure, the success the sagebrush has experienced in its invasion of the contiguous formations—grassland, desert scrub, chaparral, and woodland. The bush life-form with herbaceous branches is peculiarly fitted to adjust itself to a wide range of conditions, and while the climax is confined to a region of 5 to 10 inches of precipitation, *Artemisia tridentata* thrives in a rainfall of 20 inches when the grass competition is eliminated. Over the climax area especially, the rainfall is lowest in summer and the heaviest precipitation comes as snow during three or four winter months.

Owing to the barrier interposed by the Sierra Nevadas, the two associations differ somewhat more than is usually the case. The ecological unity of the formation is marked, as well as its general climatic harmony, but the two communities have no major dominant in common throughout. *Artemisia tridentata* is found in the eastern edge of the coastal sagebrush and *Eriogonum fasciculatum* in the xeric variety, *polifolium*, extends well into Nevada and Arizona, while *Chrysothamnus nauseosus* also occurs in both. *Salvia*, *Pentstemon*, *Isomeris*, *Atriplex*, and *Grayia* are important genera found in both but abundant in one and only relict in the other.

The Basin Sagebrush.—As a climax, this extends over the central portion of the Great Basin as already indicated, while the outstanding dominant, *Artemisia tridentata*, constitutes a low, shrubby savannah, due in large part to overgrazing, over nearly all the Palouse prairie and the intermontane portions of the mixed prairie. It often mingles with the Petran chaparral on equal terms and pushes upward into the woodland and open pine forest as a dense undergrowth. The other dominants of major importance are *Atriplex confertifolia*, *A. canescens*, *Chrysothamnus nauseosus*, *Grayia spinosa*, and *Tetradymia spinosa*. With these are a

number of undershrubs, often abundant or even controlling, such as *Artemisia trifida, arbuscula,* and *spinescens, Eurotia lanata,* and *Chrysothamnus viscidiflorus.* Practically all the dominants withstand more or less alkali and, hence, are often associated with the dominants of dry saline soil, such as *Atriplex nuttallii* and *corrugata* or of moist saline lowlands, such as *Sarcobatus vermiculatus*[275] (Figs. 236 and 237).

The Coastal Sagebrush.—As the name indicates, this community is largely confined to the Coast and Cross ranges of central and southern California and to Lower California. It is characteristic of the dry or rocky slopes of the lower foothills and is probably to be regarded as subclimax to the chaparral or as forming a postclimax savannah with the bunch-grass prairie over two-thirds or more of it area. The major dominants possess gray herbage for the most part, and, hence, this community looks much like the Basin sagebrush. The most important species are *Artemisia californica, Salvia mellifera, S. apiana,* and *Eriogonum fasciculatum,* but a large number of other shrubs play a considerable part, *viz. Pentstemon antirrhinoides, Eriodictyon crassifolium, Isomeris arborea, Rhus integrifolia,* and *Encelia californica.*

THE DESERT-SCRUB CLIMAX

Extent and Nature.—The desert scrub is more or less intermediate between chaparral and sagebrush in character, but it resembles the latter more closely in its climatic relations. As the name indicates, it is distinctly the most xerophytic of the three, the climax development taking place in a rainfall of 3 to 6 inches. The dominants are bushy shrubs, 3 to 6 feet high, as a rule, and possess the ability to produce root sprouts, to which they owe the many-stemmed habit as well as much of their dominance. The characterisitic feature that distinguishes the desert scrub from the two similar formations is the open structure of the community. The bushes stand 10 to 30 feet apart in climax portions and never form a canopy, except in the case of postclimax species like *Prosopis* and *Acacia.* The spacing is evidently a consequence of low rainfall and a correspondingly low holard, rendering a large area necessary for adequate absorption. With this is correlated the root habits of the major dominants, *Larrea,* in particular, possessing a shallow, wide-spreading system[487,506] (Fig. 261).

Like the sagebrush, the desert scrub is characterized by one great dominant, the creosote bush, *Larrea mexicana.* This further resembles *Artemisia tridentata* in extending over an area several times greater than the climax portion, forming savannah with the desert-plains grassland at the lower levels from western Texas to the Colorado Valley. The climax proper is much more restricted in area, the general limit being the isohyet of 5 inches, which coincides fairly well with the boundaries of the Gila-Sonoran, the Colorado, Mohave, and Death Valley deserts.[327] Here the characteristic dominants are but two, *Larrea* and *Franseria dumosa,*

the former 2 to 4 feet tall and evergreen, the latter a bushy undershrub, 1 to 2 feet high and with drying persistent leaves. In the numerous washes, *Hilaria rigida*, a shrubby grass, is a typical dominant that often

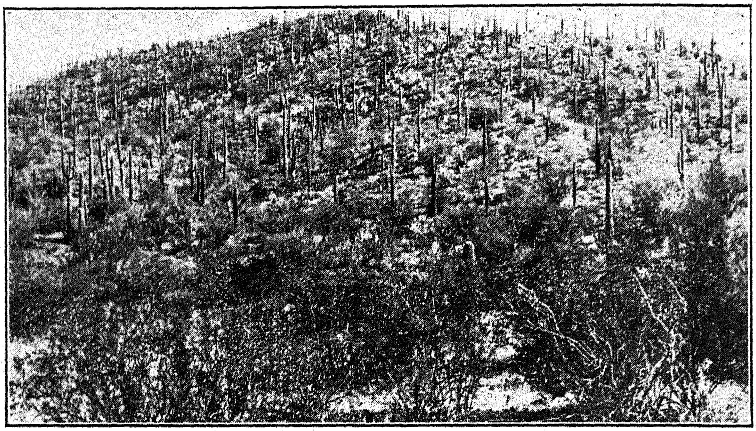

FIG. 261.—*Cereus-Encelia* subclimax on a lava ridge with *Larrea* below, Tucson, Ariz.

takes part in the full climax, while *Acacia, Prosopis, Parkinsonia, Dalea,* and *Chilopsis* mark the deeper and less arid valleys (Fig. 262).

Subclimaxes of the Desert Scrub.—It was formerly supposed that this formation comprised two associations, an eastern and a western, but

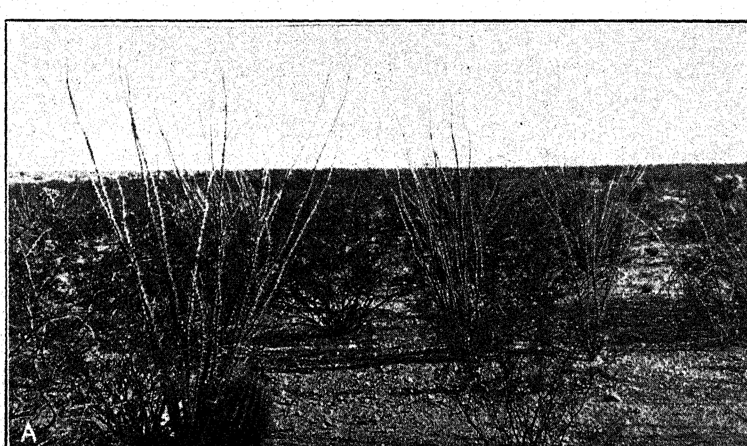

FIG. 262.—*Fouquiera* subclimax in *Larrea* plain, Tucson, Ariz.

the former has been proved to be a desert-plains savannah in which the shrubs *Larrea, Flourensia, Franseria deltoides, Ephedra, Condalia, Opuntia, Acacia,* and *Prosopis* have largely replaced the grasses in consequence of overgrazing and of fire, also, to some extent. Protected places usually

exhibit *Bouteloua*, *Aristida*, and their associates as dominants, and wet seasons when the grazing pressure is lessened serve to reconstruct the desert plains in graphic fashion. Where the rainfall is regularly 12 to 15 inches, the dominant rôle of the grasses is beyond question, and the spacing of the low shrubs becomes much more open, a result also significant of protection against grazing.

In addition to the bronze scrub or *Larrea-Flourensia* associes is a taller and more massive subclimax found in southwestern Texas and adjacent Mexico. This consists of *Acacia*, *Condalia*, *Celtis*, and *Prosopis* as major dominants and has all the appearance of a true climax. A study of the effects of fire and grazing, however, and of the course of succession makes it clear that this so-called *mesquite*, no matter how luxuriant and controlling, is really a subclimax associes that has greatly increased in extent during the historical period. In nature, it is essentially postclimax, and other postclimaxes occur on escarpments, talus slopes, and rocky hills from western Texas to Mexico and eastern California. In the east this is known as *sotol*, an associes of *Agave*, *Dasylirion*, *Nolina*, *Yucca*, and *Opuntia*, while in Arizona and Mexico it comprises the thorn scrub, consisting of *Cereus*, *Fouquiera*, *Parkinsonia*, *Acacia*, *Opuntia*, and similar spiny shrubs[483] (Figs. 242 and 262).

Climax Map of North America.—This map is diagrammatic to a high degree, with the object of emphasizing the general relations and extent of the various climaxes. No attempt has been made to delimit these with accuracy, partly because of the small scale, but also because most of the information from remote regions especially has not taken the climax and subclimax into account. The scale has likewise made it necessary to exaggerate the width of narrow strips, such as the alpine tundra, and to ignore the many isolated peaks with this climax. Furthermore, the same color has not only been employed for the montane and subalpine climaxes, but the woodland and chaparral have necessarily been included in this. Savannah has been regularly included in the grassland climax, and the areas of sagebrush and desert scrub correspondingly reduced. The intimate relations of the several mountain climaxes, the position and extent of the associations within each formation, and the approximate boundaries of the many communities involved can only be exhibited by means of a large wall-chart, which is now in preparation.

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